Saproxylic invertebrates in plantation forests

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Abstract

The conversion of natural forests to production land uses has led to huge losses of biodiversity and continues to threaten remaining terrestrial flora and fauna throughout the world. The global demand for wood products and energy, which was partly responsible for the loss of primary native habitat, is now one of the leading drivers of afforestation with significant new areas of plantation replacing former agricultural lands. While plantations do not support the same biodiversity values as natural forests they do provide significant habitat for a range of species. Saproxylic invertebrates (species that are dependent on deadwood) are strongly affected by the temporal and spatial availability of different deadwood resources. Previous research on saproxylic invertebrates has largely been restricted to natural or managed natural forests predominantly in the Northern Hemisphere, where forest management practices have been modified to conserve these species This thesis fills a distinct research gap in New Zealand and is the first large scale study to quantify the effects of deadwood age, wood species, and landscape composition on saproxylic invertebrates in our plantation forests by direct rearing. In this thesis I show that thinning residues, which are currently retained in many plantation forests, provide significant habitat for a range of native invertebrate taxonomic groups, including diverse assemblages of Coleoptera and Hymenoptera. Deadwood age is an important attribute determining taxonomic richness of saproxylic invertebrates. Richness of invertebrate orders/classes and Coleoptera species all increased in older deadwood material, and a stepwise multidimensional analysis procedure indicated that the age of deadwood was the most important factor structuring saproxylic invertebrate community composition in *Pinus radiata* thinning residues. Deadwood age was a stronger predictor of community composition in thinning residue than measures of landscape composition, such as the proportion of remnant native forest cover. The change in saproxylic

invertebrate composition that occurs with deadwood age was related to changes in the feeding guilds, with a transition from primary wood feeding species to predators/parasitoids and fungal feeders with increasing dead wood age. Because thinning's are carried out at prescribed times throughout the stand rotation, stand age could be adopted as a proxy for deadwood age in these systems allowing forest managers a simple method for monitoring saproxylic beetle habitat availability . My research provides strong empirical evidence that supports the existing conservation paradigm that forest managers should seek to create a mosaic of habitats at the landscape scale to enhance biodiversity opportunities in plantations.

In addition to the habitat opportunities provided by *P. radiata* deadwood that is derived from silvicultural practices there are several sources of native wood in plantations. Native woody resources are found in either the embedded remnant areas of native forest or in the understory of stands as many native woody species colonise this habitat. As yet the importance of native understory deadwood resources for saproxylic species is unknown. In addition it is unclear how the importance of such understory resources is influenced by proximity to remnant native forest patches. I used experimental wood billets of four tree species (3 native and the exotic *P. radiata*) placed along replicated transects spanning native habitat and adjacent early stage regenerating plantation stands to assess the saproxylic invertebrate assemblages associated with different deadwood species as a function of proximity to native forest. I found that an interaction between wood host specificity (local scale) and proximity to interior native forest (landscape scale) was the most important factor regulating saproxylic invertebrate community structure. Deadwood of the native subcanopy trees *Schefflera digitata*, *Melicytus ramiflorus*, *Aristotelia serrata* and the exotic conifer *P. radiata* provided habitat for different subsets of the saproxylic fauna. The most pronounced differences in saproxylic community structure were between the native sub-canopy broadleaf species and

the exotic *P. radiata*. Surprisingly the *P. radiata* supported a greater species richness and abundance of saproxylic Coleoptera in native remnants than the native wood species in the same habitat. In general, species richness was higher in native forest habitats and declined with increasing distance from native habitat. These results suggest that both the diversity of deadwood resources that are available and their proximity to native remnants are important for maintaining saproxylic communities in plantations. However, two of the native wood species (*M. ramiflorus* and *A. serrata*) exhibited steep declines in species richness at the plantation native forest boundary, suggesting that the contrasting stand types (native remnant and young regenerating plantation stands) with their different microclimate may have had a significant influence. Future research needs to compare the saproxylic fauna of dead wood in mature plantation stands with adjacent native remnants to ascertain if the effect of native habitat proximity is due to landscape composition or a reflection of microclimatic differences.

The large diversity of saproxylic species observed during this study highlights the importance of plantations as habitat for saproxylic species, particularly in heavily fragmented landscapes that retain little original native forest. My research findings provide forest managers with options for improving forest management to enhance opportunities for the conservation of saproxylic invertebrates. In addition my thesis provides one of the most comprehensive multi-taxon data sets of saproxylic species associated with a variety of deadwood resources. This information will be invaluable to future researchers that continue to work on New Zealand's saproxylic fauna.

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Chapter 1 General introduction

1.1 Saproxylic organisms and their ecological functions

Saproxylic invertebrates are species that are dependent on, i.e., live on and inside decaying wood and by definition they rely on the availability of dead wood to complete some stage of their lifecycle (Speight 1989). They may use dead wood directly as habitat or strictly rely on an interaction with other organisms that do. Saproxylic invertebrates provide important ecosystem services such as decomposition of woody debris and leaf litter, pollination, and natural predator control (Reichle 1977, Lavelle et al. 2006). These saproxylic species may contribute to the direct physical breakdown of dead wood through feeding and tunnelling, or they may indirectly facilitate decay by vectoring spores and enabling colonisation of wood decay fungi (Müller et al. 2002, Persiani et al. 2010). Studies have shown strong empirical evidence for interactions between beetle and fungi in the decay process, revealing patterns of joint colonization and correlations between the beetle and fungal diversity in decaying wood (Lindhe and Lindelow 2004, Persiani et al. 2010). Aside from the important ecological roles of saproxylic invertebrates and their intrinsic values, they may also have important interactions with other more charismatic organisms. For example, saproxylic insects feeding on fungi in dead wood have high nutritional value, and higher trophic levels, such as the North Island brown and the great spotted Kiwi (*Apteryx mantelli* and *A. haasti* respectively) can gain benefit directly and indirectly from these organisms by feeding on them and their invertebrate predators (Kleinpaste 1990, White 1993).

1.2 Plantation forestry and saproxylic organisms

The increasing extent of plantation forests is not a new phenomenon and in past centuries many natural forests in Europe were converted to plantations of exotic conifers (Speight 1989). In the last decade, planted forests (of which intensive plantation are a subset of) have been increasing at a rate of 5 million ha per year (FAO 2010). Along the production forest management intensity gradient the large scale removal of vegetation and replacement with exotic tree plantations has the most discernable and detrimental effect on species richness and community composition (Paillet et al. 2010). However, recently plantations have been established on agricultural sites (Brockerhoff et al. 2008b) which provides opportunities for biodiversity conservation that would not be possible with other production land use options, particularly where native forests are rare (Norton 2001, Pawson et al. 2008). As such, researchers have realised the potential biodiversity benefits that plantations can provide (Norton 1989, Ogden et al. 1997, Brockerhoff et al. 2005, Brunet et al. 2011), and that research is needed to quantify how specific land management practices impact biodiversity (Lindenmayer et al. 2006, Müller et al. 2010).

The reduction in natural forests continues and plantations continue to expand which is expected to continue into the future (FAO 2010). The increasing extent of plantation forests and increasing demand for forest products and bioenergy creates a trade-off between conservation and production (Hartley 2002, Jonsson et al. 2005, Bengt 2006). Increasing management intensity by removing dead wood, which in the past would have been retained (such as stumps), will increase productivity but may be detrimental to the saproxylic organisms that rely on this resource (Lassauce et al. 2011). However, the relative importance of land use intensity and specific habitat attributes is unclear as Jacobs et al. (2007) found that harvesting explained less variation in beetle assemblages than specific habitat attributes

of dead wood. Thus, further work is required to determine the relative importance of land use intensity and specific deadwood attributes and how they interact.

The impact of forest management differs between taxonomic groups of organisms that rely on continuity of habitat, large trees and the availability of dead wood. These orgainisms, such as saproxylic beetles, are the most negatively affected by forest management (Paillet et al. 2010). The effects of management practices on saproxylic invertebrates, particularly beetles, has been the focus of much research because of their sensitivity to management practices that alter the dynamics of dead wood quantity and quality (Langor et al. 2008, Müller et al. 2010). Because of this sensitivity, their functional importance and diversity, saproxylic invertebrates have been suggested as indicators of sustainable forest management in Canada (Langor and Spence 2006). However, their application as indicators in many countries is hindered by the lack of expertise required for species identifications and knowledge of their taxonomy and ecology. In New Zealand Hutcheson et al. (1999) have suggested that beetles are ideal indicators of terrestrial biodiversity and ecosystem functioning because of their high diversity and knowledge of their taxonomy and ecology. However, the argument is relatively complex, the large number of undescribed species, particularly from important saproxylic groups such as Cerambycidae (subfamily Lamiinae) and the Elateridae, make the use of saproxylic Coleoptera as indicators more challenging.

Some have suggested dead wood variables, that have performed well for saproxylic species (Brin et al. 2009) are a more cost effective method than the use of species based indicators (Juutinen et al. 2006). Specifically the quality and quantity of coarse woody debris have been suggested as better predictors of beetle abundance and richness than landscape factors, such as the distance to reserves and stand size (McGeoch et al. 2007). However, measures of landscape structure have been suggested as indicators of sustainable forest management

because they are less context dependent than site based dead wood elements that need to be verified on a case by case basis (Banks-Leite et al. 2011). Two key landscape scale processes are the distribution of reserves (often referred to as “set asides”) and the spatial distribution of different aged deadwood resources that are created by thinning and harvesting operations. Given the uncertainty between landscape or site scale processes, research is required to assess how biodiversity can be maintained in plantation forests at scales that are relevant to plantation forest managers and how the success of such strategies should be measured.

1.3 Plantation forests and decomposition of coarse woody debris

The chemical and physical properties of dead wood (including thinning material), such as nutrient concentrations as well as initial wood density, are known to change with time (Ganjegunte et al. 2004, Garrett et al. 2008, Garrett et al. 2010). Such physical changes are mirrored by biological changes such as the occurrence of specific saproxylic species. For example, age - followed by density - was the strongest predictor of the occurrence of wood boring beetle larvae in decaying tree snags (Saint-Germain et al. 2007). Many studies have shown that the decomposition stage of deadwood has a significant effect on the composition of the saproxylic invertebrate diversity (Vanderwel et al. 2006, Brunet and Isacsson 2009, Thomas et al. 2009). In particular different trophic guilds tend to dominate at different stages in the wood decay process (Vanderwel et al. 2006). For example, fungal feeders and predators are more abundant in older tree stumps (Hjältén et al. 2010). In addition to changes in trophic guilds, beetle species richness may also change along the deadwood decay gradient (Hammond et al. 2004, Ulyshen and Hanula 2010). Arthropod richness was shown to peak in young wood due to a diverse assemblage of primary wood feeding bark beetles, wood borers and their predators in North American aspen wood (Ulyshen and Hanula 2010). However, this pattern is not universal as others have shown that species richness increases in older

decay stages (Heilmann-Clausen 2001, Vanderwel et al. 2006, Brunet and Isacsson 2009, Thomas et al. 2009), perhaps because there are a greater variety of niches to explore, thus facilitating a more diverse fauna (Langor et al. 2008).

The provision of suitable microhabitats, such as wood in different decay stages, has been encouraged despite a lack of clear empirical evidence for any specific management interventions which create such micro-habitats (Davies et al. 2008). Although, much research has focused on studying changes in saproxylic communities related to decay stages of deadwood (Heilmann-Clausen 2001, Vanderwel et al. 2006, Brunet and Isacsson 2009, Thomas et al. 2009) the age of dead wood is a more relevant metric that can be applied by forest managers, particularly as silvicultural operations are carried out at defined points in forest rotation. Therefore, the age of deadwood derived from these operations is known and the spatial distribution of deadwood is closely correlated to the distribution of different aged stands. If deadwood age provides a suitable proxy for deadwood decay stage and proves to be a suitable indicator of saproxylic diversity it would be readily adapted by forest managers and spatially optimised at a landscape scale.

1.4 Host specificity and proximity to native habitat

Habitat loss and fragmentation (the breaking apart of habitats) are critical agents of species decline (Sala et al. 2000, Fahrig 2003, Ewers and Didham 2006). Understanding the mechanistic basis for changes in population and community dynamics as a result of habitat fragmentation is hindered because fragmentation is imbedded in processes such as habitat loss and land use intensification (Ewers and Didham 2006). For example, edge effects extend far into forest fragments surrounded by grassland, however they may be less extreme when fragments are embedded in a structurally similar matrix, such as plantation forests (Ewers and

Didham 2008, Pawson et al. 2008, Campbell et al. In Press). Edge responses are altered by matrix type, indeed many species appear to utilise plantation forests to a greater extent than the pasture matrix (Campbell et al. In Press). In New Zealand, plantations often have fragments of un-managed native habitat imbedded within them, therefore native species within these areas have the ability to utilise the surrounding plantation forest as an extension to their native range (Brockerhoff et al. 2008a, Langer et al. 2008). Species composition in mature plantations as opposed to recently harvested plantations and pastures is most similar to that in native forests (Pawson et al. 2008, Brunet et al. 2011). However, even recently harvested stands may provide some resources for saproxylics because of the abundance of deadwood, which is closely related to saproxylic arthropod assemblages in natural canopy gaps in Europe (Müller et al. 2008, Müller et al. 2010). Furthermore, forest edges have altered coarse woody debris dynamics because of increased mortality of large trees (Laurance et al. 1998, Nascimento and Laurance 2004), yet no research has quantified edge effects in saproxylic invertebrate communities and how they interact with resource availability.

Overseas many studies of saproxylic organisms have realised the importance of deadwood tree species in structuring saproxylic communities (Lindhe and Lindelow 2004, Lindbladh et al. 2007, Jie et al. 2008, Kebli et al. 2011). Most of this research has compared different stump species in mixed forests (Lindhe and Lindelow 2004, Lindbladh et al. 2007). However, in New Zealand 90% of plantation forests are composed of even aged stands of *Pinus radiata* that are managed by clearfelling (Anon 2010). Although such plantations are managed to produce one tree species they are not strictly monocultures as they may contain a rich native flora of understory woody species if moisture is not limited (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003, Brunet et al. 2011). As yet, no one has extended these findings to assess how the deadwood derived from such understory tree species influences the

diversity of other tropic groups. Because the greatest differences in the composition of saproxylic communities between tree species has been found between coniferous and broadleaved species (Lindhe and Lindelow 2004, Jie et al. 2008), it is likely that native broadleaf understory tree species, such as *Schefflera digitata*, *Aristotelia serrata* and *Melicytus ramiflorus* (which are common in the understory of New Zealand plantations (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003)), will be important in structuring the composition of saproxylic invertebrates in stands.

1.5 Thesis objectives

My thesis aims to quantify how attributes of plantation forests affect the ecology of invertebrates reliant on dead wood. Specifically, I will study how the age of decomposing *P. radiata* affects the composition and distribution of invertebrate communities in New Zealand plantation forest landscapes (Chapter 2). My research will also assess how landscape scale factors (edge gradient effects) interact with resource requirements of saproxylic species (wood host preferences) and how these attributes effect the structure and distribution of saproxylic invertebrate assemblages (Chapter 3). By determining the relative importance of local and landscape scale attributes (and interactions between them) my research will provide guidance to improve the conservation of saproxylic species in plantation forests. In addition to the pure research questions, my experiments contribute valuable baseline data about the composition, ecology and spatial distribution of saproxylic invertebrates in New Zealand as little is currently known about many species.

The thesis is presented as three chapters, the first two being written as scientific manuscripts for future submission to peer-reviewed journals. These chapters have appendices which will serve as online supplements. The final chapter is an overall synopsis of my findings. These

are integrated with a focus on the implications of my findings to plantation forest management. I have attempted to keep repetition to a minimum; however, there is inevitably some overlap between data chapters because the topics researched are closely related.

Chapter 2: *Maintaining spatial heterogeneity to promote biodiversity conservation in plantations – niche partitioning in decomposing wood*

To determine how saproxylic invertebrate communities respond to the age of decaying *P. radiata* thinning residues in plantations I used a standardized space for time substitution (chronosequence) in plantation forests of the Kaingaroa Plateau in the central North Island of New Zealand.

Chapter 3: *Local and landscape scale effects on saproxylic invertebrates – deadwood species and native forest proximity effects in a plantation forest landscape*

To quantify saproxylic invertebrate community composition utilising different dead-wood species across native and plantation forest boundaries I reared saproxylic invertebrates from experimental wood billets placed across transects spanning native forest remnants and adjacent plantation forest stands. This was to determine the effect that native habitat proximity has on saproxylic invertebrates and how this interacts with the resource requirements of saproxylic invertebrates, i.e., different species of deadwood.

Chapter 4: *General discussion*

In this final chapter I summarise my results from the previous chapters and present these findings in the context of their application to plantation forest management. I also explore the potential directions for future research and plantation forest management.

Chapter 2 Conservation benefits of spatial heterogeneity through invertebrate succession in decaying deadwood in a plantation forest

2.1 Introduction

Habitat loss is a critical driver of biodiversity loss and is expected to continue as the human population expands (Sala et al. 2000, Fahrig 2001, Brook et al. 2003). Natural forests have been greatly reduced in their spatial extent and this is a trend that continues with total forest loss averaging 13 million ha per annum between 2000 and 2010 (FAO 2010). Despite this overall loss of forests, plantation forests have expanded by an average of 5 million ha per annum between 2000 and 2010 throughout the world to meet market demands for timber and fibre (FAO 2010). Given the limited extent of protected natural areas in many landscapes, the need to integrate biodiversity conservation into production land uses is becoming increasingly apparent (Norton 2001, Watson et al. 2011). Plantation forests can provide surrogate habitat for many species, including native birds (Deconchat et al. 2009, Clout and Gaze 1984, Barbaro et al. 2005, Seaton et al. 2010), understory plants (Allen et al. 1995, Díaz et al. 1998, Brockerhoff et al. 2003, Brunet et al. 2011), and invertebrates (Mesibov 2005, Berndt et al. 2008, Pawson et al. 2008). Some of these species play important functional roles within forests in general, such as dung beetles and leaf-litter detritivores that contribute to nutrient-cycling processes, although many of these taxonomic groups can be severely impoverished in plantation forests (Barlow et al. 2007, Gardner et al. 2008, Paillet et al. 2010, Meijer et al. 2011). Despite such reduced diversity, plantations can be the only significant source of forest habitat available in some landscapes, thus conservation research needs to address how opportunities to enhance biodiversity can be improved in plantation forests (Brockerhoff et al. 2005, Pawson et al. 2008, Meijer et al. 2011).

In the severely fragmented landscapes of New Zealand, 25% of all forest habitat is comprised of exotic plantation forests (Anon 2010). Intensively-managed plantation forests, consisting primarily of *Pinus radiata*, have been referred to in the past as "biological deserts", and are viewed by many as homogeneous landscapes (Stephens and Wagner 2007). However, these ecosystems have been shown to support significant native biodiversity, particularly in the understory (Hartley 2002, Lindenmayer and Hobbs 2004, Carnus et al. 2006, Brockerhoff et al. 2008a). Plantations are also known to support a number of threatened species, including charismatic fauna such as the North Island brown kiwi (*Apteryx mantelli*), great spotted kiwi (*A. haasti*) , and long-tailed bat (*Chalinolobus tuberculatus*) (Borkin and Parsons 2009, Pawson et al. 2010). In exceptional circumstances plantations might even provide the only remaining habitat for a species. For example, the endemic New Zealand carabid beetle *Holcaspis brevicula* is only known to occur in Eyrewell Forest, an exotic *P. radiata* plantation (Brockerhoff et al. 2005). Not all production land uses have equivalent impacts on native biodiversity and native habitat specialists, such as some invertebrates, which are more likely to utilise adjacent closed canopy plantation stands than the wider pastoral landscape (Didham 2011, Meijer et al. 2011, Campbell et al. In Press).

Invertebrates are a vital component of forest biodiversity. They perform important ecosystem services such as pollination, provide natural predator control, and are vital to the decomposition processes of leaf litter and woody debris (Reichle 1977, Lavelle et al. 2006). In production forest landscapes there has been a particular focus on the role of saproxylic invertebrates (species that are reliant on dead wood to complete their lifecycle (Speight 1989)) that are directly or indirectly involved in wood decomposition processes (Müller et al. 2002, Hood et al. 2004, Persiani et al. 2010). Saproxylic arthropods may contribute to the direct physical breakdown of dead wood through feeding and tunnelling, or they may

indirectly facilitate decay through the colonisation of wood decay fungi (Müller et al. 2002, Persiani et al. 2010). For example, the bark beetles *Hylastes ater* and *Hylurgus ligniperda* have been shown to vector fungi in *P. radiata* plantations in New Zealand, while other bark beetles have been shown to be important vectors of fungi in European forests (Reay et al. 2005, 2006, Persson et al. 2011).

Saproxylic invertebrates are sensitive to forest management practices that alter the spatial and temporal availability of deadwood resources (Bishop, 2009). As such, they are ideal indicators of some aspects of sustainable forest management (Grove 2002, Langor and Spence 2006). Individual saproxylic species often rely on specific dead wood attributes, such as tree species identity, decay stage, or level of light exposure (Jonsell et al. 1998). Because forest management often results in a reduction in the availability of dead wood and a simplification of the deadwood structures in production forests, many species of saproxylic invertebrates are threatened (Grove 2002, Hjältén et al. 2010). Those with low dispersal ability that are reliant on long term habitat continuity are most at risk from forest management practices, particularly harvesting (Bishop et al. 2009, Buse 2011). Two broad suites of strategies have been proposed to enhance saproxylic biodiversity in managed forests. Firstly, those that focus on mitigating adverse stand-level management practices, such as retaining stumps and snags and maintaining understory vegetation, and secondly those that focus on enhancing landscape-scale processes, such as alternative tree species and the size and distribution of cutovers (Lindenmayer and Hobbs 2004, McGeoch et al. 2007, Brockerhoff et al. 2008a, Thomas et al. 2009). It is difficult to determine the relative importance of these two alternative conservation strategies. However, stand factors, such as the quality and quantity of coarse woody debris, were found to be more important than

landscape factors, such as distance to the nearest reserve, in a Swedish boreal forest landscape (McGeoch et al. 2007).

An important regulator of saproxylic invertebrate community composition is the decay stage of wood (Saint-Germain et al. 2007, Langor et al. 2008). Wood decay stage is a fine scale attribute, however in plantations it represents a stand level attribute as thinning and harvesting are carried out more or less uniformly at a stand scale. Therefore, the distribution of coarse woody debris decay stages, and subsequently the invertebrate fauna associated with these decay stages at a landscape scale, is determined by stand level management practices.

Globally, there have been numerous studies of saproxylic invertebrate succession as a function of deadwood age in both managed natural forests and plantation forests (Heilmann-Clausen 2001, Jonsson et al. 2005, Saint-Germain et al. 2007, Ulyshen and Hanula 2010, Kebli et al. 2011). Broad decay stage classifications have been devised as a substitute for direct measures of deadwood age as it is often difficult or impossible to determine, particularly in natural systems (Maser et al. 1979, Fraver et al. 2002). Some studies use as little as two decay stage classes (Thomas et al. 2009) and even using four classes may not capture all of the variation associated with the different stages of wood decay (Vanderwel et al. 2006). The key problem with subjective decay stages is that there is no robust relationship between decay stage class and the actual age of the deadwood. An alternative approach has been to repeatedly sample logs over time, which overcomes problems associated with sampling from different spatial locations (Ulyshen and Hanula 2010, Grove and Forster 2011). However, this approach requires long term studies and results can be confounded by the seasonal or climatic conditions that precede sampling. Another approach is to use a space-for-time substitution (chronosequence) approach and identify coarse woody debris of known age using some other information source such as a temporal sequence of aerial photographs

(Heilmann-Clausen 2001) or data from the harvesting and thinning records of forestry companies. The advantage of using forestry data is that it is possible to obtain highly precise estimates (to the month) of the age of deadwood within a stand, so that different-aged deadwood can be sampled at a single point in time under consistent environmental conditions.

In this study, I used a chronosequence approach to quantify how saproxylic invertebrate community composition and abundance changed with the age of dead wood. Unlike previous studies (Vanderwel et al. 2006, Saint-Germain et al. 2007, Thomas et al. 2009)my approach has allowed me to quantify changes in the saproxylic invertebrate fauna through time across a large scale plantation forest landscape with unprecedented accuracy of deadwood age. Although decay stage classes may be more ecologically relevant under some circumstances, plantation management record dates of harvesting and thinning operations allow age of deadwood to be a more relevant measure for landscape management, as it can be optimised on a spatial basis to achieve conservation outcomes in a plantation. The use of saproxylic invertebrates as indicators of sustainable forest management practices is often hindered by a lack of knowledge about their diversity, ecology, abundance, and response to forest management. In some countries, such as Sweden, stand-level initiatives to conserve saproxylic species are now mandatory in production forests (Grove 2002, Lindhe and Lindelow 2004). However, this is not the case in many other parts of the world, including New Zealand.

This study is the first investigation of the arthropod fauna associated with different dead wood age or even decay stages of wood in any New Zealand forest type, and the results of this study will inform conservation managers about the habitat requirements (in terms of dead wood resources) of native invertebrate biodiversity. It is likely that particular species will be

associated with different-aged dead wood resources, thus niche partitioning along the decay gradient will lead to variation in the community structure of deadwood communities in the different aged wood. As deadwood ages, there is an increase in the diversity of microhabitats, and as such I expect older deadwood to have the highest species richness of invertebrates.

2.2 Methods

2.2.1 Study Region

The study was conducted on the Kaingaroa Plateau in the central North Island of New Zealand. The region lies within an area of intensive volcanism where fluvial processes formed dissecting gullies on a predominantly flat plateau composed of silicic Taupo tephra and basaltic Tarawera tephra (Froggatt and Lowe 1990). The area is prone to drought because the soil profile is primarily composed of loose unweathered basaltic scoria with poor moisture holding capacity (Molloy 1988).

All of the study sites were established within plantation forests dominated by the exotic conifer *P. radiata*. Before logging and burning, this area was covered with Podocarp-broadleaved forest (Nicholls 1991), remnants of which are scattered throughout the plantation forests as small regenerating forest fragments (Figure 2.1). The altitude of sites ranged from 61 – 429 m a.s.l, with mean annual temperature ranging from 11.5 – 13.6 °C (Terralink 2004). Precipitation in the area ranges from 1200 – 1600 mm/yr which predominantly falls as rain; however the area averages one snowfall per year that never accumulates (Quayle 1983). The distribution of this precipitation is influenced by topography and proximity to the coastline (Quayle 1983).

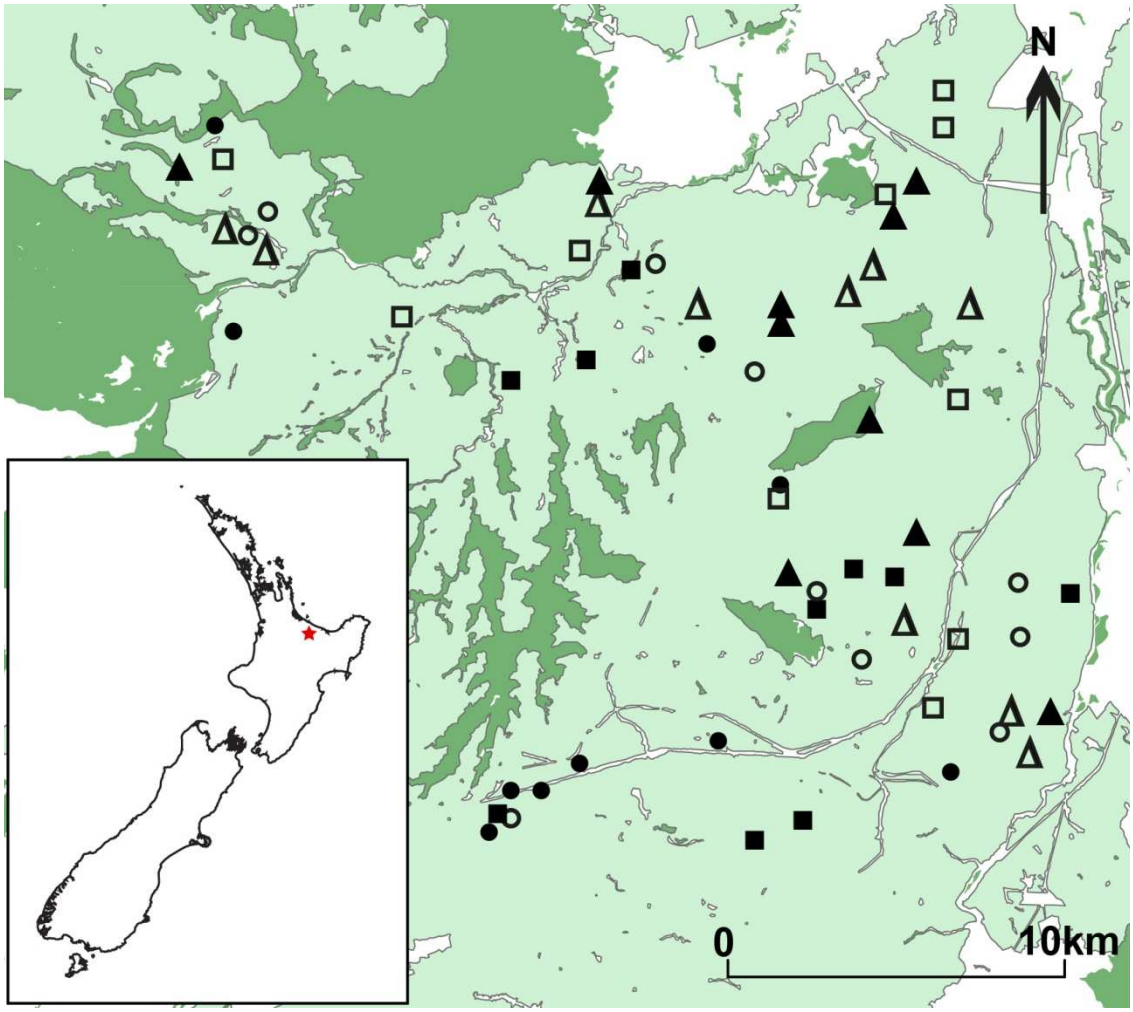


Figure 2.1: Spatial location of dead wood sampling sites in six decay classes, 1 yr (●), 2 yr (○), 4 yr (■), 6 yr (□), 8 yr (▲) and 10 yr (Δ). Areas covered with plantation forest are indicated by light green, areas of remnant native forest are indicated by a darker green and white areas represent open habitats such as native and exotic grassland. Study area location within insert of New Zealand coastline is indicated with star symbol.

2.2.2 Site Selection

Sixty even-aged *P. radiata* stands (average size 56 ha (± 6 ha S.E.) in area) were selected using geospatial forestry land management data provided by participating forestry companies. Ten replicate stands were identified of each of six different ages, with stem thinning occurring at nominal time intervals of either 1, 2, 4, 6, 8, or 10 years prior to 9th September 2009 (see Table 2.1). Most selected stands were within 3 months of the defined age category. If enough replicate stands were not available for a given age class the criteria were expanded but none of the age classes overlapped. In *P. radiata* plantations in the central North Island, thinning residues older than 10 years of age become crumbled and fragile, retaining only 21% of their original mass (Garrett et al. 2008), making them almost impossible to sample. Care was taken to ensure a random distribution of replicate stands of each age class across the study area, to minimize potential spatial autocorrelation between deadwood age and sampling location (potential spatial autocorrelation effects were tested in the statistical analyses).

Table 2.1. The number of days since saplings were thinned of nominal treatment categories assigned to represent deadwood age within each stand. Age-class boundaries were drawn to create non-overlapping categories.

	Age class of dead wood					
Replicate	1 year	2 year	4 year	6 year	8 year	10 year
1	180	592	1298	2012	2846	3634
2	243	650	1358	2091	2900	3665
3	268	650	1361	2134	2903	3704
4	274	678	1387	2144	2907	3706
5	319	702	1532	2158	2911	3706
6	321	854	1540	2159	2967	3706
7	413	855	1540	2230	2968	3760
8	442	856	1571	2272	2973	3764
9	442	978	1576	2293	3028	3944
10	527	*	1589	2311	3056	4309

* sample was lost

2.2.3 Collection of wood billets

From each stand, one 30-cm long section of log (referred to as a 'billet', see Figure 2.2) was collected from each of three randomly-selected thinned trees that were close to or on the ground. Fallen trees were examined to ensure that they were thinned trees, rather than trees that had died of natural causes (e.g., historical windthrow). When stands were known to have undergone multiple thinning events, the age class of trees of interest were identified by comparing log diameters. Trees selected were at least 20 m from the stand boundary, with billets cut at least 15 cm from the tree base, or in the case of older decay classes at least 15 cm from any break in the stem and at a position along the stem where the diameter was 15cm. Wood billets were collected in two sampling periods which were from 12 to 20 December

2009 and 14 to 22 January 2010. Five stand replicates of each age class were sampled in each sampling period.

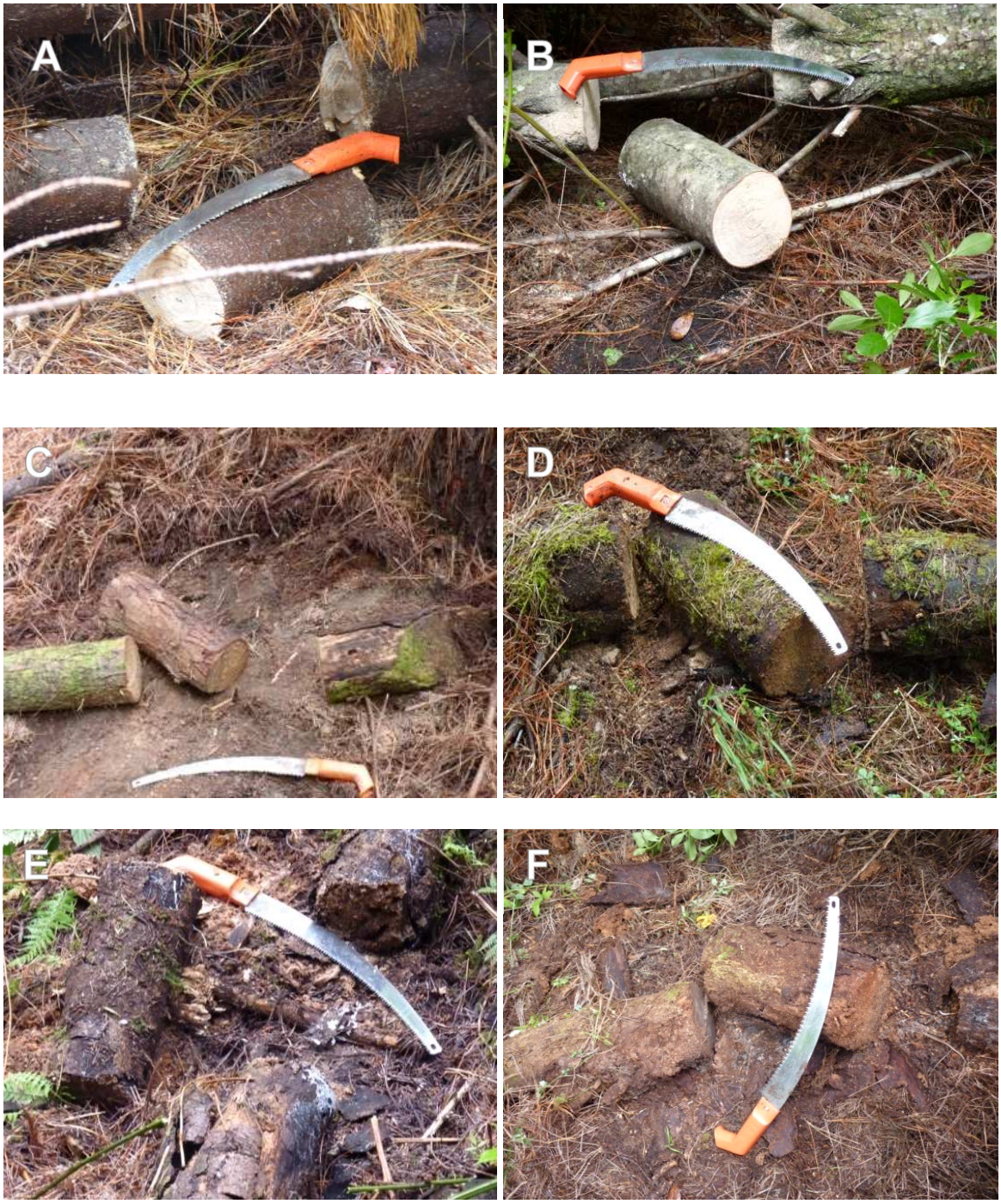


Figure 2.2. Representative examples of 1, 2, 4, 6, 8 and 10 year old billets (a – f, respectively) show that they are quite different habitats. Initially (a, b) the deadwood is intact and attacked by small beetles such as Scolytinae feeding on phloem (Savely 1939). As supporting branches break the log comes into contact with the ground (c, d) and decomposition is significantly increased (Garrett et al. 2010). Eventually (e, f) large chunks of bark start to come loose and the wood takes on a darker hue due to high fungal activity (McCarthy et al. 2010), and large emergence holes appear where wood

boring beetles such as *Prionoplus reticularis* have emerged. Such empty galleries and sub cortical spaces under bark provide habitat for late successional species (Savely 1939).

2.2.4 Insect Rearing

It has been shown that a greater abundance of invertebrates are captured using onsite emergence traps (Ulyshen and Hanula 2010). However, this is an expensive and time consuming method, particularly with such widely distributed sampling sites (Hammond 1997). The methodology I used to rear insects was consistent across all treatments and is a simple and efficient method to provide a direct measure of saproxylic invertebrate composition (Ulyshen and Hanula 2009a). Studies of management effects on biodiversity have often been based on species which occur in plantations, but are not necessarily breeding there (Lindenmayer and Hobbs 2004). My approach overcomes this limitation as rearing provides a direct association between the species and their habitat.

Billets were individually bagged in thick sealed paper bags and transported to an emergence facility (within 24 hours). The three billets taken from each stand were wrapped together in bird-stop netting to limit the break-up of the fragile older decay-stage billets (Figure 2.3 A), and then all three were placed inside one hanging plastic emergence bag that was sealed to prevent insect escape (or enter from the outside) (Figure 2.3 B). Any invertebrates found on the glass sorting table while billets were being prepared for transfer to the emergence facility were placed inside the emergence bag and the table was swept clean before preparing the next sample. Each bag was aerated for 20 minutes every 6 hours to prevent a build-up of moisture and mould. Air was supplied by a medium pressure blower (Imasu, model CAD5-35). Invertebrates emerging from the billets were collected in a jar at the bottom of the emergence bag, which contained 150 ml of monoethylene glycol (Figure 2.3 C). Invertebrates

were reared for approximately 6 months (range: 177 – 186 days; see Table 2.2) after which the contents of the collecting jar was transferred to 70% ethanol for storage prior to sorting.

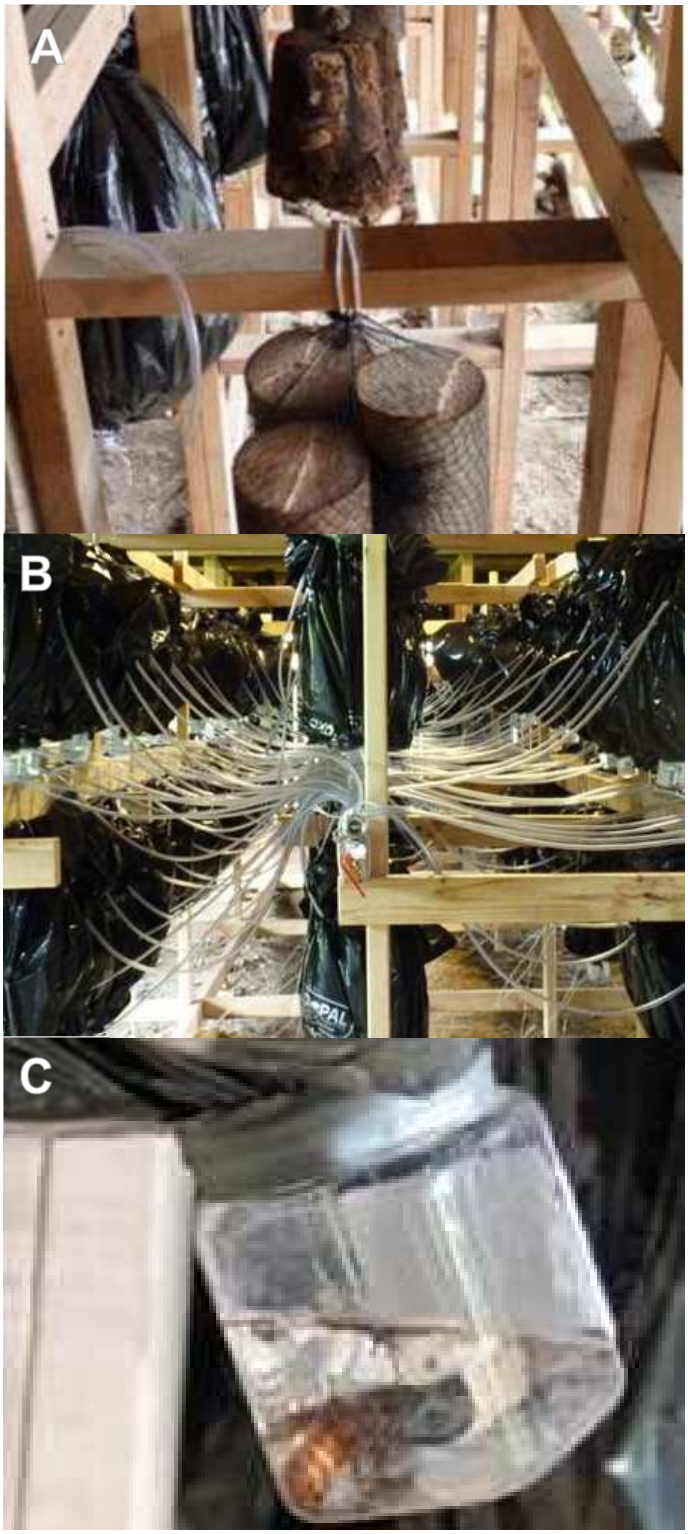


Figure 2.3. A) Three pooled billet logs were initially hung in bird stop netting (Fruitfed Supplies). This netting was selected to ensure that large invertebrates such as *Prionoplus reticularis* (Cerambycidae), New Zealand's largest beetle, would be able to pass through unimpeded. B) These were enclosed in black plastic emerging bags and (C) Collecting jar at bottom of bag with an adult of *P. reticularis*.

2.2.5 Insect Identification

Invertebrates were initially sorted to taxonomic class or order, and then selected taxa (Diptera, Coleoptera, Hymenoptera (Formicidae), Hymenoptera (other), Hemiptera and Diplopoda) were separated into separate vials for future species-level sorting. Remaining classes and orders were picked and stored together in a single vial, except Collembola and Acari which were left in the remaining 'by catch' with other non-invertebrate debris such as insect frass.

In this study, Coleoptera and Hymenoptera were identified to morphologically identifiable taxonomic units ('morphospecies') with representative specimens pinned for each species. A reference collection is housed at the Scion, Ilam Office in Christchurch. All beetle morphospecies were checked by an experienced entomologist (Stephen Pawson, Scion), and where possible species names were assigned by Stephen Pawson and Stephen Thorpe (Auckland University, Honorary Research Associate). Hymenoptera were identified to morphospecies and where possible species names were assigned by Darren Ward (Landcare Research).

2.2.6 Environmental co-variables

Environmental co-variables that may influence patterns in invertebrate community structure were extracted from geospatial data layers using Arc Map 9.3.1 (ESRI, Redlands, USA). Geospatial data layers of plantation stand information were provided by participating forest management companies and the spatial locations of native forest remnants were extracted from the New Zealand Landcover Database (LCDB2) (Terralink 2004). Mean annual

temperature data were extracted from the underlying Land Environments of New Zealand data layers. A full list of measured environmental variables is given in Table 2.2.

Table 2.2. Description of environmental variables and units of measurement.

Variable	Explanation	Unit of measure
Age of dead wood	Categorical age class	Years
Latitude	Latitudinal distance from centroid of all study sites	Metres
Longitude	Longitudinal distance from centroid of all study sites	Metres
Native 100	Proportion of native habitat within a 100m radius (ranging from 0.00 to 0.28)	Proportion
Native 200	Proportion of native forest habitat within a 200m radius (ranging from 0.00 to 0.29)	Proportion
Native 500	Proportion of native habitat within a 500m radius (ranging from 0.00 to 0.25)	Proportion
Native 1000	Proportion of native habitat within a 1000m radius (ranging from 0.00 to 0.20)	Proportion
Native 2000	Proportion of native habitat within a 2000m radius (ranging from 0.00 to 0.13)	Proportion
Native 5000	Proportion of native habitat within a 5000m radius (ranging from 0.00 to 0.21)	Proportion
Thin number	First or second thinning	Binary
Thin type	Waste (thinning residue left in situ) or extraction (thinning residue removed)	Binary
Prune history	Tended or untended	Binary
Collection period	Identifies two periods of collection (12/12/09 to 20/12/09 and 14/01/10 to 22/01/10.	Binary
Rotation	The number of silvicultural cycles (one, two or three)	Integer
Stocking	The density of stems in the stand	Stems per hectare
Year planted	The year the stand was established	Years AD
Mean annual temperature (MAT)	Mean annual temperature of the site	℃
Days emerging	The time in days from when billet was hung in a rearing facility and when the invertebrate sample was collected. This ranged from 177 days to 186 days.	Days
Forest	Tarawera, Kaingaroa or Matahina	Categorical

2.2.7 Data Analysis

Species Richness

Sample-based rarefaction was conducted using the analytical approach of Colwell (Colwell et al. 2004) using EstimateS version 8.2.0 (Colwell 2006).Species accumulation curves were rescaled to the number of individuals collected, as recommended by (Gotelli and Colwell 2001). To compare expected species richness between different dead wood age classes a cubic polynomial function was fitted to each species accumulation curve and subsequently evaluated at the lowest equivalent number of individuals present in each data set (invertebrate orders; Coleoptera and Hymenoptera) to provide a direct point of comparison that is not affected by abundance.

Community Composition

Community composition analyses were conducted in a step-wise process starting with an unconstrained ordination followed by evaluation of environmental variables to select those that were subsequently used in a final constrained multivariate analysis. All beetle species and orders with less than 2 individuals were removed from the dataset to reduce potential undue influence from rare species. An initial unconstrained Non-metric Multidimensional Scaling (NMDS) was conducted in R with the function *metaMDS* in the vegan 1.15-3 package. This function allows the user to select the number of dimensions (k) to be analysed. There are no set selection criteria for choosing appropriate values of k (Anderson and Willis, 2003). The analysis was run repeatedly on the three data sets (invertebrate orders, Coleoptera and Hymenoptera species) using Bray-Curtis dissimilarities with sequentially higher levels of k until the reduction in stress was less than 1.5 from the previous k level. Ordinations were run using 999 permutations of the raw data matrix. Once the model with the appropriate k

level was determined the *envfit* command from the vegan 1.15-3 package was used to assess the correlation of environmental variables (see Table 2.2) to the position of different aged wood samples in the NMDS ordination.

Significant environmental variables that represented potential spatial autocorrelation in site effects (including MAT, year forest was planted, forest and collection period) were partialled out as covariables in constrained nonparametric multivariate analyses of variance. This analysis tested the effect of deadwood age (as a continuous variable) on ordinal, Coleoptera and Hymenoptera community structure using the following parameters: ln(x+1) transformed species abundance data, Bray-Curtis dissimilarities and 9999 permutations of the raw data using DistLM (Anderson 2001, 2004).

Identification of individual species responses

Invertebrate orders, Coleoptera species and Hymenoptera species were tested for associations with specific aged dead wood using the indicator value (*IndVal*) approach in the R labdsv 1.4-1 package. Indicator values are a robust quantitative method of identifying species that are characteristic of a particular treatment group that is chosen a-priori (Dufrêne and Legendre 1997). Species with strong indicator values for specific dead wood age categories (indicator values over 0.30) were further analysed to quantify the change in abundance of these species as a function of deadwood age.

Species traits

Feeding groups (xylophage, fungivore, predator/parasite, or scavenger) and the origin of species (native or exotic) were assigned to each beetle species (See Appendix 2.0). Because some recognised taxonomic units were only identified to family level, and there is a lack of

specific knowledge about the ecology of many saproxylic species in New Zealand, it was not possible to assign beetles to a feeding group or origin and many beetles had to be classed as unknown. A Chi square test was used to test if the proportion of beetles in each feeding group was independent of deadwood age, and if the proportion of native or exotic beetles was independent of deadwood age.

2.3 Results

2.3.1 Species Richness

A total of 19,844 individuals were extracted from the 177 log billets (one emergence bag containing three billets was lost during processing; Table 2.1) and sorted to 23 taxonomic classes and orders (Table 2.3). This included 1,999 beetles (Coleoptera adults) and 1,284 wasps and ants (Hymenoptera adults) that were subsequently sorted to morphospecies groups (99 species of Coleoptera and 17 species of Hymenoptera).

Ordinal taxon richness increased progressively with the age of deadwood and was significantly higher in 8 and 10 year old decay classes than in the 1 and 2 year decay classes (based on 95% confidence limits) (Figure 2.4a). Changes in beetle species richness did not exhibit a general trend with increasing age of deadwood, however 1 year old deadwood had significantly lower species richness than all other decay classes (based on 95% confidence limits) (Figure 2.4b). Hymenoptera species richness was not influenced by the age of deadwood (Figure 2.4c).

Table 2.3. Total abundance of taxonomic classes and orders emerging from different age classes of dead wood.

Taxonomic group	**Age class of dead wood**						
	1 year	2 year	4 year	6 year	8 year	10 year	Total
Diptera	991	1260	1825	1777	1094	511	7458
Collembola	282	597	961	1230	1038	235	4343
Coleoptera	903	337	518	362	530	199	2849
Acari	228	155	746	739	616	253	2737
Hymenoptera	126	32	312	173	177	452	1272
Diplopoda	10	28	117	125	129	82	491
Isoptera	0	0	0	34	56	76	166
Lepidoptera	65	4	3	1	12	9	94
Hemiptera	0	13	12	37	12	14	88
Chilopoda	1	4	19	5	26	6	61
Dermaptera	0	10	19	22	2	5	58
Araneae	1	1	1	30	11	5	49
Mollusca	0	5	9	10	5	5	34
Pseudoscorpiones	1	0	3	7	15	5	31
Isopoda	0	0	1	3	12	12	28
Opiliones	0	0	0	8	11	3	22
Orthoptera	0	0	6	4	3	3	16
Amphipoda	0	0	0	1	2	11	14
Psocoptera	3	5	0	4	2	0	14
Annelida	0	3	0	1	3	1	8
Thysanoptera	6	0	0	0	0	0	6
Platyhelminthes	0	0	0	1	2	0	3
Blattodea	0	0	1	1	0	0	2
Total	2617	2454	4553	4575	3758	1887	19844

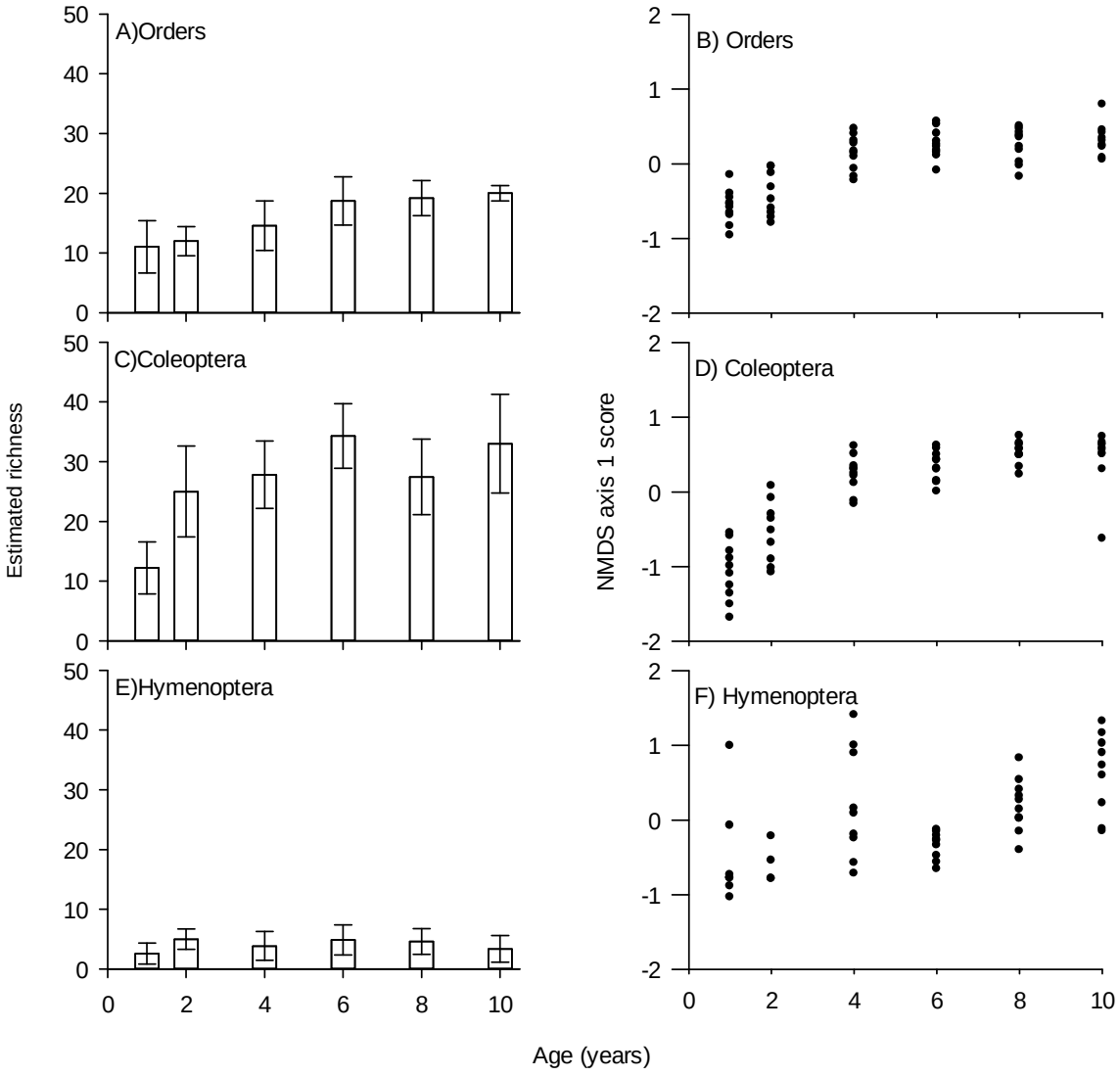


Figure 2.4. Estimated species richness (rarefaction) of (A) invertebrate orders (2161 individuals), (B) Coleoptera species (161 individuals), and (C) Hymenoptera species (33 individuals) as a function of dead wood age. Sample scores from the primary axis (axis 1) of an NMDS analysis showing changes in community composition of, (D) invertebrate orders, (E) Coleoptera species, and (F) Hymenoptera species as a function of dead wood age.

2.3.2 Community Composition

Ordinal level

Invertebrate ordinal community composition was most distinct in 1 and 2 year old deadwood (Figure 2.5). Deadwood age was the strongest predictor of change in invertebrate composition at the ordinal level (Table 2.4). This is reflected in the change in community composition as expressed by axis one sample scores as a function of increasing deadwood age (Figure 2.4B). The timing of billet collection in the field and mean annual temperature of the site (MAT) were both significant predictors of ordinal composition while spatial location, stand age and collection period and the proportion of native habitat in the landscape of various scales were not (Table 2.4). To remove the effect of significant, potentially confounding environmental factors, MAT and collection period were incorporated as covariables in a multivariate multiple regression test by permutation (DISTLM). This analysis confirmed that deadwood age remained a highly significant predictor and explained 11.13% of the variation in ordinal composition ($F_{1, 55} = 7.4484$, $P < 0.0001$) (Table 2.5).

Coleoptera

Removing species with abundance of 2 or less left a data set consisting of 1944 individuals and 62 species. Beetle community composition varied strongly between different deadwood age classes and was most distinct in young (1 and 2 year old) age classes (Figure 2.5B). Age was again the strongest predictor of changes in beetle species composition (Table 2.4, Figure 2.4D). The year planted, MAT and forest were also significant predictors of community composition but the proportion of native habitat in the landscape was not significant at any spatial scale (Table 2.4). Incorporating MAT and the year the plantation stand was planted as covariables in a multivariate multiple regression test by permutation (DISTLM) confirmed

that deadwood age remained a highly significant predictor and explained 10.58% of the variation in beetle community composition ($F_{1, 54} = 7.3$, $P < 0.0001$)(Table 2.5).

Hymenoptera

Hymenoptera were only present in 48 of the 59 invertebrate samples. Removal of rare species with 2 individuals or less left a data set consisting of 1,262 individuals belonging to 21 species. Hymenoptera community composition was highly variable and compositional changes as a function of deadwood age were less clear than those expressed by either the invertebrate orders or Coleoptera (Figure 2.5A-C). Despite this, age significantly explained 47% of the variation in community composition before constraint (Table 2.4). No other environmental variables were significant predictors of Hymenoptera community composition (Table 2.4). Although deadwood age was a significant predictor of Hymenoptera species composition, it only explained 1.52% of the variation in Hymenoptera species composition after constraint ($F_{1, 47} = 0.72461$, $P < 0.0015$) (Table 2.5).

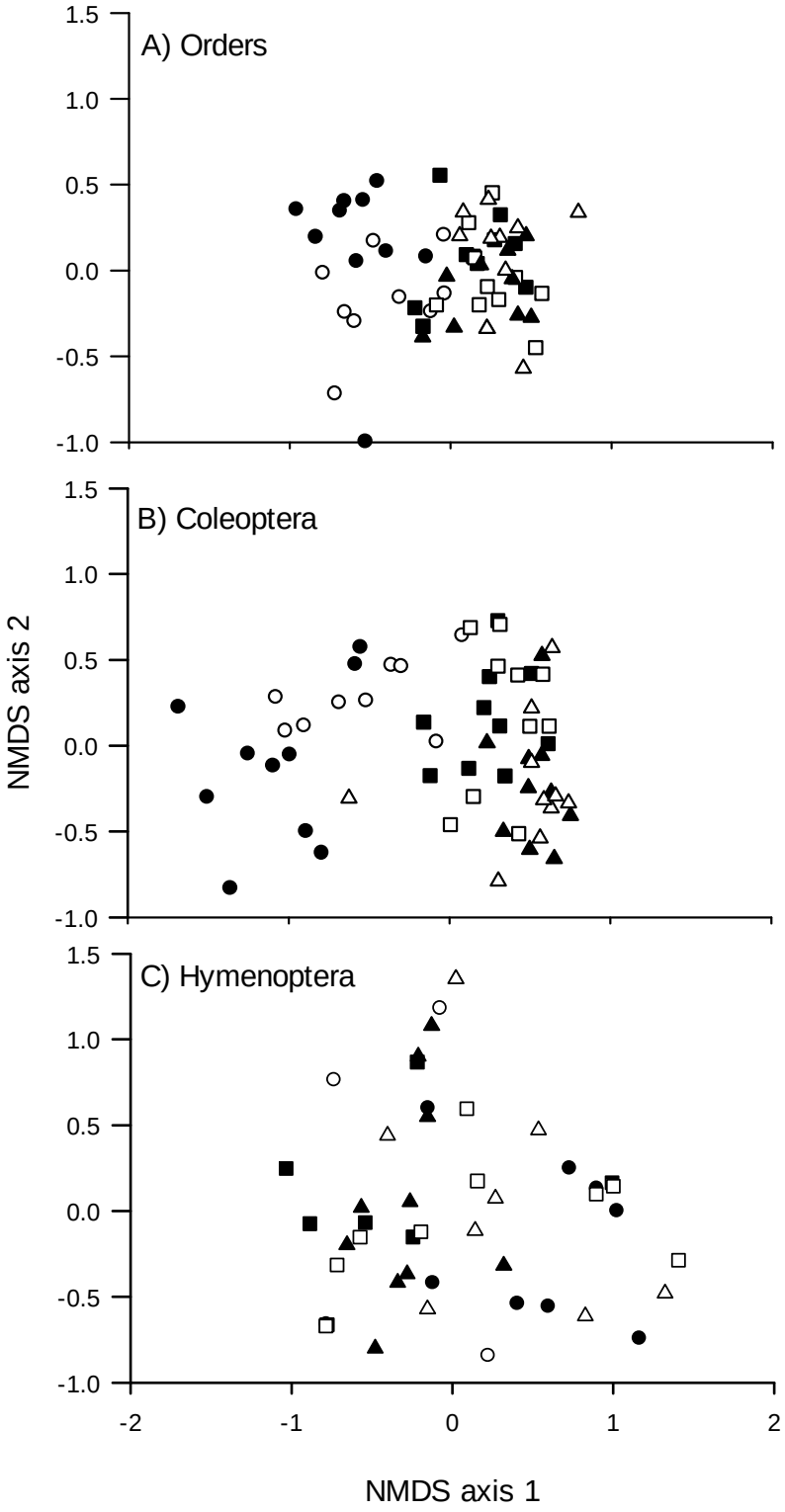


Figure 2.5. Community composition of different aged wood (1 yr (●), 2 yr (○), 4 yr (■), 6 yr (□), 8 yr (▲) and 10 yr (Δ)) visualised as NMDS axis one and two scores of; A) invertebrate orders (K= 7

dimensions, stress =7.04), B) Coleoptera species (K= 6 dimensions, stress = 9.06) and C) Hymenoptera species (K = 7 dimensions, stress = 5.56).

Table 2.4. Correlation of environmental variables to the NMDS analysis of community structure. Significance levels are indicated by "***" ≤ 0.001, "**" ≤ 0.01 and "*" ≤ 0.05.

	Invertebrate Orders			Coleoptera			Hymenoptera		
Variable	**r2**	**Pr(>r)**		**r2**	**Pr(>r)**		**r2**	**Pr(>r)**	
Age of dead wood	0.685	0.001	***	0.680	0.001	***	0.473	0.001	***
Latitude	0.048	0.910		0.077	0.100		0.156	0.402	
Longitude	0.123	0.428		0.049	0.252		0.027	0.995	
100m buffer	0.039	0.999		0.009	0.845		0.173	0.210	
200m buffer	0.017	0.999		0.003	0.916		0.130	0.517	
500m buffer	0.053	0.902		0.015	0.663		0.057	0.947	
1000m buffer	0.083	0.709		0.003	0.912		0.068	0.894	
2000m buffer	0.050	0.916		0.006	0.858		0.080	0.825	
5000m buffer	0.098	0.621		0.003	0.930		0.037	0.972	
Thin number	0.229	0.058		0.054	0.212		0.048	0.945	
Thin type	0.054	0.906		0.020	0.596		0.177	0.277	
Prune history	0.111	0.495		0.095	0.052		0.164	0.331	
Collection period	0.242	0.031	*	0.004	0.898		0.177	0.277	
Rotation	0.038	0.954		0.019	0.600		0.152	0.392	
Stocking	0.124	0.405		0.042	0.316		0.135	0.508	
Year planted	0.119	0.440		0.211	0.002	**	0.194	0.217	
Mean annual temperature	0.258	0.022	*	0.180	0.005	**	0.229	0.125	
Days emerging	0.092	0.647		0.011	0.730		0.104	0.703	
Forest	0.043	0.238		0.150	0.008	**	0.058	0.143	

Table 2.5. Anova (DISTLM) results showing the variation in community structure of invertebrate orders, Coleoptera species and Hymenoptera species explained by deadwood age after controlling for significant covariables (Table 2.4). Note: there were no significant covariables for Hymenoptera species composition. Significance indicated by "***" ≤ 0.001, "**" ≤ 0.01, "*" ≤ 0.05.

Source of variation	df	MS	SS	pseudo-F	P-value	Variation explained
Order						
Covariables	2	2663	-	-	-	-
Dead wood age (df)	1	4442	4442	7.4	0.0001***	0.11
Residual error (df)	55	32797	596			
Total	58	39901				
Coleoptera						
Covariables	3	22966	-	-	-	-
Dead wood age (df)	1	22005	22002	7.3	0.0001***	0.11
Residual error (df)	54	163077	3020			
Total	58	208048				
Hymenoptera						
Dead wood age (df)	1	2617	2617	0.7	0.0015**	0.02
Residual error (df)	47	172335	169718	3611		
Total	48					

2.3.3 Individual order and species responses

Indicator species analysis showed that 5 orders, 13 Coleoptera species and 3 Hymenoptera species were strongly associated with specific deadwood age classes (Table 2.6). At an ordinal level Coleoptera were strongly associated with one year old logs, whereas Araneae, Isopoda, Hemiptera and Amphipoda were strongly associated with late decay stage classes (Figure 2.6a-c and Appendix 2.0). These associations of specific orders with different aged decomposing dead wood are also exhibited at the species-level by individual species of Coleoptera (Figure 2.6d-f) and Hymenoptera (Figure 2.6g-i) that have similar associations with specific ages of dead wood.

Of the seven beetle species associated with early dead wood decay stages (1 and 2 years old), five were primary wood feeders, one was a fungal feeder and one was a predator/parasitoid (Appendix 2.0). Of the seven beetle species associated with older dead wood decay stages (4 – 10 years old), two were wood feeders, 2 were fungal feeders and three were predator/parasitoids (Appendix 2.0). The seven beetle species associated with older dead wood decay stages had lower maximum indicator values than species in the younger age classes (Table 2.6). They were also present in a wider range of deadwood age classes, with all seven species being present in at least four different age classes. In contrast, beetle species associated with one and two year old deadwood age classes had stronger indicator values (Table 2.6,Figure 2.6: D and G). These strong indicator values for one and two year old decay classes is consistent with the NMDS ordination diagrams for orders and Coleoptera that show a clear separation in ordination space from later deadwood decay classes (Figure 2.5: A and B).

Table 2.6. Number of significant ($P \leq .05$) indicator taxa for (A) taxonomic orders, (B) Coleoptera species, and (C) Hymenoptera species in each deadwood age class. The range in the indicator value for each comparison is given in parentheses. Full indicator results for all taxa are given in Appendix 2.0.

Age class (years)	A) Invertebrate order	B) Coleoptera species	C) Hymenoptera species
1	1 (0.32)	4 (0.30 - 0.93)	1 (0.38)
2		3 (0.22 - 0.30)	
4		2 (0.25 - 0.34)	
6	2 (0.38 - 0.43)		1 (0.42)
8	1 (0.30)	5 (0.28 - 0.36)	
10	1 (0.31)		2 (0.35 - 0.46)

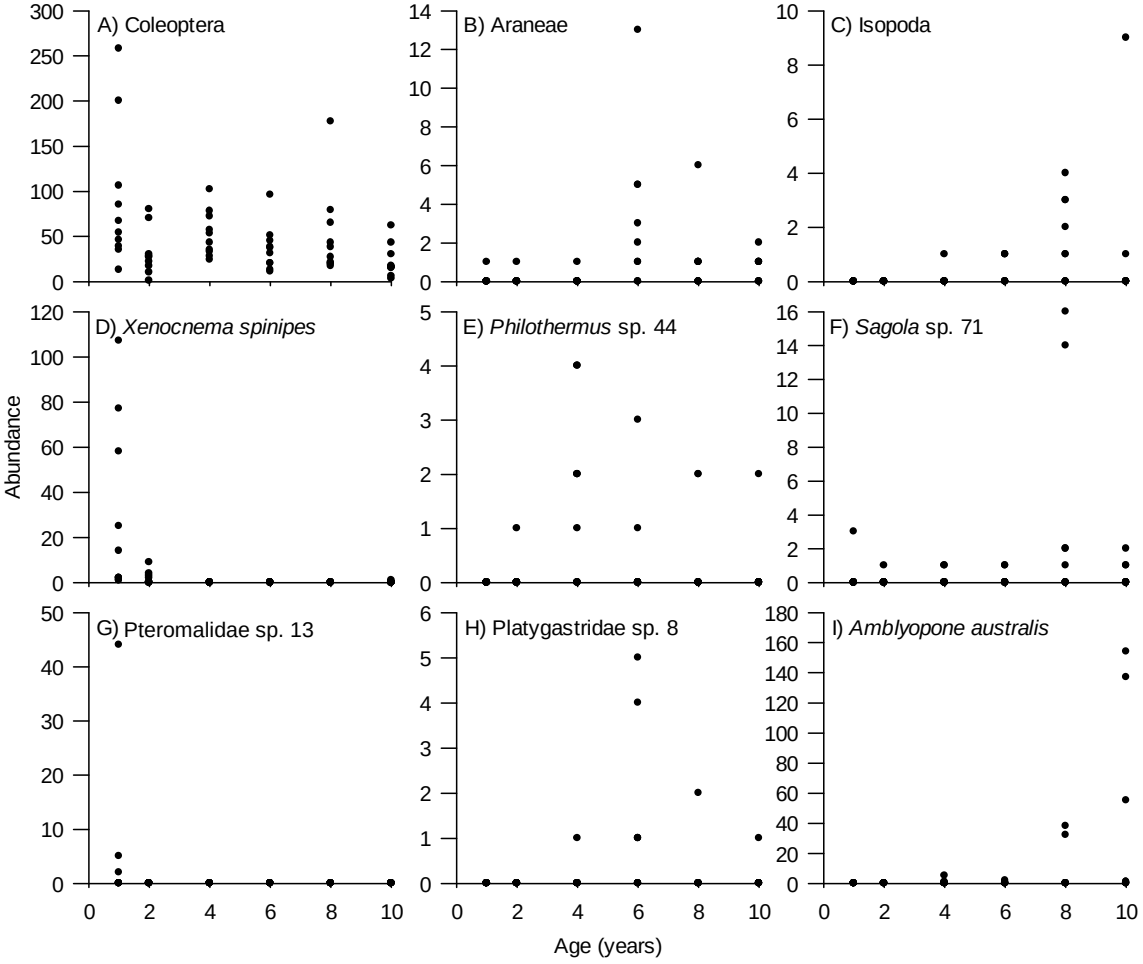


Figure 2.6. Abundance of selected orders and species with significant indicator preference for different age categories of deadwood. Strength of indicator values and their significance are; A) 0.32 *, B) 0.43**, C) 0.30*, D) 0.93***, E) 0.34**, F) 0.37*, G) 0.38*, H) 0.42**, I) 0.46* (see Appendix 2.0 for full list of indicator species values).

2.3.4 Species Traits

Dead wood age had a significant effect on the abundance of beetles in different feeding groups (Chi Squared Test, Chi = 418, df = 10, p-value ≤0 .001). The abundance of wood feeders in one and two year old dead wood was greater than expected, whereas in older deadwood age classes the fungal feeders and predators/parasitoids were more abundant than expected (Table 2.7). The increased relative frequency of fungal feeders was most pronounced in the 8 to 10 year age classes and the increased relative frequency of predators/parasitoids was most pronounced in the 4 to 10 year age classes (Table 2.7). The frequency of beetles that were native or exotic was also significantly influenced by the age of dead wood (Chi = 111, df = 5, p-value ≤ 0.001). However, this result must be interpreted with caution as there were low expected counts in some categories (Wild, 2000). All 26 exotic beetle individuals found in this study emerged from one and two year old dead wood, with the majority present in age class 1 (Table 2.7).

Table 2.7. Observed number of individuals in different trophic feeding groups (scavengers were excluded because there were too few observations) and with different origins (native or exotic) across dead wood age classes. Expected values based on a chi square contingency table are given in brackets.

	Feeding Group			Origin	
age	**wood**	**fungi**	**predator/parasitoid**	**native**	**exotic**
1 yr	367 (225)	25 (41)	4 (130)	58 (77)	24 (5)
2 yr	126 (85)	3 (16)	20 (49)	22 (23)	2 (1)
4 yr	191 (219)	38 (40)	156 (126)	134 (127)	0 (7)
6 yr	99 (154)	21 (28)	152 (89)	82 (77)	0 (5)
8 yr	164 (246)	74 (45)	196 (142)	123 (116)	0 (7)
10 yr	88 (106)	30 (20)	69 (61)	27 (26)	0 (1)

2.4 Discussion

Conserving biodiversity in plantation forests relies on accurate data about how forest management practices impact native biodiversity, but there is a lack of relevant research showing how specific management interventions impact biodiversity at a scale that is relevant to plantation forest managers (Lindenmayer et al. 2006). By using a standardised space-for-time substitution over a large plantation forest landscape, here I show that richness of invertebrate communities (invertebrate orders and Coleoptera species) in thinning residues increases with time since dead wood was created. Parallel with this increase in richness there is a turnover of species composition with the age of dead wood, where distinct assemblages occupy different stages of the decomposition gradient. There is a shift in the relative abundance of Coleoptera species from different feeding groups as a function of deadwood age. Young deadwood is dominated by individuals feeding primarily on the wood itself, however the relative abundance of predators/parasitoids and fungi feeders increases with deadwood age. The changes in richness and community structure I observed as a function of different aged *P. radiata* thinning residues is congruent with overseas research that found clear changes in saproxylic arthropod and fungal communities as a function of different decay stages of other types of dead wood (Heilmann-Clausen 2001, Vanderwel et al. 2006, Brunet and Isacsson 2009, Thomas et al. 2009). The exact drivers of these patterns of community succession are unclear, but are probably related to biologically and physically mediated changes in wood properties that change during the process of decomposition (Savely 1939, Heilmann-Clausen 2001, Ganjegunte et al. 2004, Persson et al. 2011). Such changes in wood properties are likely to be the result of an interaction between the actions of arthropods and fungi (Persiani et al. 2010). The clear patterns I observed provide strong empirical evidence that the creation of different aged deadwood resources through

management practices will facilitate greater biodiversity across plantation forest landscapes. This supports previous advice given to forest managers that they should seek to create mosaics of different aged stands in the landscape (Grove 2002, Hartley 2002, Brockerhoff et al. 2008a).

2.4.1 Invertebrate species richness increases with dead wood age

There was a clear increase in ordinal and species richness in older *P. radiata* dead wood. Many other studies have found increases in the diversity of fungi and arthropods at medium and late stages of wood decay (Heilmann-Clausen 2001, Hammond et al. 2004, Saint-Germain et al. 2007, Thomas et al. 2009, Grove and Forster 2011). This is typically thought to be due to greater structural variation in older wood (Saint-Germain et al. 2010) as the wood decomposes leading to greater abundance and diversity of wood rotting fungi and micro-habitats (Lindhe et al. 2004, Langor et al. 2008). Increases in richness after the early stages of decay are probably then due to a greater number of niches for a fauna that have specific physical and biotic habitat requirements which are not related to the species of wood. My findings are contrary to the high species richness of beetles observed on young rather than older wood in dead Aspen(Ulyshen and Hanula 2010). This may be due to the fact that most of the exotic species colonised young logs and the lower richness we observed in young pine logs may be attributable to the fact that species colonising freshly-fallen wood are often host specific (Jie et al. 2008, Ulyshen and Hanula 2010) and as *P. radiata* is an exotic species in New Zealand there may not have been a great diversity of host-specific phloem feeders capable of attacking this wood at my study sites.

2.4.2 Community structure varies with dead wood age

The strong correlation of observed changes in community structure of Orders and species of Coleoptera and Hymenoptera are consistent with other studies of the community structure of saproxylic invertebrates. Log variables, such as age and decay stage are known to influence the community composition of macrofungi and slime moulds (Heilmann-Clausen 2001), Coleoptera, Hymenoptera and Diptera species (Vanderwel et al. 2006, Brunet and Isacsson 2009). However, landscape factors such as distance to the forest edge have been shown to be comparatively unimportant (Heilmann-Clausen 2001). These findings are consistent with my conclusion that landscape variables (proportion of native forest habitat in the surrounding landscape) were comparatively unimportant compared to log age in structuring saproxylic communities. Of course, it should be noted that this study was not specifically designed to capture the full range of variation in proximity of plantation stands to remnant native forests, or other components of variation in landscape structure. Nevertheless, there was a strong gradient in the proportion of native habitat and the age of coarse woody debris was clearly more important in structuring saproxylic invertebrate communities, even after controlling for the confounding effects of temperature and season of collection.

2.4.3 Drivers of change in community structure

The lack of basic biological and ecological knowledge about most species and the impacts of forests management on population dynamics are major limitations for the maintenance of biodiversity in managed forests (Jonsson et al. 2005, Langor and Spence 2006). Habitat or resource specialists are the most sensitive to forest management because they rely on particular forest features (Paillet et al. 2010, Brunet et al. 2011). Thirteen of the 99 species of Coleoptera were clearly associated with particular deadwood age classes; these species may

be the most sensitive to the availability of specific aged thinning residues. Order and species correlations with specific aged logs across the entire gradient of decomposition suggests different saproxylic species and taxonomic groups have different resource and habitat requirements which change across different aged dead wood. Given that there are species with strong associations for all deadwood age classes it is important to maintain a variety of dead wood ages within the landscape to sustain the full suite of species. Current management practices that create large scale clearfells maybe acceptable for a selection of species with good dispersal abilities, but a shift to smaller clearfells may improve habitat connectivity and persistence of species with poor dispersal abilities (Pawson et al. 2012, Pawson et al. 2009).

The abundance of species which are associated with specific dead wood ages probably relies on biotic interactions with other saproxylic organisms, such as fungi or prey availability, or on particular physical and chemical attributes of the dead wood (Savely 1939). For example, indicator species associated with freshly-fallen wood may feed on phloem, but this resource is quickly consumed (and/or deteriorated) after which the habitat is no longer suitable for such species (Ulyshen and Hanula 2010). These early colonists, such as *Xenocnema spinipes*, can have mandibular cavities which probably serve to transport associated fungi (Crowson 1984). Other species, such as *Hylurgus ligniperda*, are known to be associated with several fungal species that infect *P. radiata* dead wood (Reay et al. 2006). Therefore, the actions of the early colonizing species are likely to facilitate the colonization of species typical of older deadwood that rely on fungi as a source of food, the log as a habitat for shelter, or to prey on other invertebrates (Savely 1939).

In Canada and Europe, the occurrence of saproxylic invertebrates in coarse woody debris has been related to changes in the nutritional and physical parameters of wood that occur as it decays (Saint-Germain et al. 2007). These same factors may be responsible, at least in part,

for the observed changes in species associations with different aged wood seen in this study. For example, the concentration of nitrogen in *Pinus radiata* wood increases over time, whereas wood density and carbohydrate availability decreases over time (Ganjegunte et al. 2004, Garrett et al. 2008, Garrett et al. 2010). Nitrogen is a limiting nutrient because it is required for building proteins and some species are unable to survive on a low nitrogen diet (White, 1993). However, it has also been suggested that correlations in the occurrence patterns of Cerambycidae larvae in older dead wood might also be due to neutral mechanisms, i.e. spatiotemporal autocorrelation of insect occurrence (Saint-Germain et al. 2007). This could explain peaks within the tolerable range of dead wood age for some organisms, but given that we found indicator species for each age class of dead wood that was studied, there must be some trait-specific determinants of saproxylic invertebrate occurrence patterns.

2.4.4 Succession of feeding groups

The relative abundance of primary wood feeding insects was greatest in young dead wood whereas predators/parasitoids and fungal feeders were most abundant in older dead wood. Other studies have found that insect communities in young logs and snags are comprised of high numbers of primary wood feeders and their associated predators and parasites (Gibb et al. 2006, Vanderwel et al. 2006, Johansson et al. 2007). The phloem and cambium resources these groups rely on are quickly used up which explains the decline in the relative abundance of wood feeders in older aged logs (Ulyshen and Hanula 2010). Conversely, in later decay stages of stumps and logs there is an increase in beetles that feed on fungi (Vanderwel et al. 2006, Hjältén et al. 2010), which is present in greater abundance and diversity in older wood (Heilmann-Clausen 2001, Persiani et al. 2010). Predators are also more common in older dead wood material (Vanderwel et al. 2006, Thomas et al. 2009, Hjältén et al. 2010). This

rich community of predatory species is probably supported by a higher abundance of prey in old logs and an overlap with the subterranean fauna as logs come into greater contact with the ground. In addition, the internal structures of the wood break down to create a more complex diversity of microhabitats. This was exemplified by the occurrence of the generalist predatory ant, *Amblyopone australis*, which is primarily subterranean (Haskins and Haskins 1951) but was strongly associated with older classes of dead wood that were in contact with the ground and contained internal cavities for nesting.

2.4.5 Further research and implications for management

Species and order richness increased over the age range of logs studied. However, decomposition is slower in larger diameter dead wood material and varies significantly between species of wood (Beets et al. 2008, Garrett et al. 2008, Garrett et al. 2010). For example the average decay half-life of New Zealand native hard wood logs created in a windfalls associated with a storm is 30 years (Beets et al. 2008), while that for stems from thinning slash in these plantation forests is only six years (Garrett et al. 2008). It has been shown that old, large logs harbour high levels of biodiversity (Grove and Forster 2011), however it is unknown if this applies to intensively managed exotic plantation species such as *P. radiata* in New Zealand. Species associated with large dead logs are known to have poor dispersal abilities and require the greatest habitat continuity (Siitonen and Saaristo 2000, Langor et al. 2008). Further research needs to assess the importance of larger post-harvest material, such as un-merchantable logs and stumps and their importance for conservation of saproxylic species in plantations.

It has been suggested that storm damage drives dead wood availability, structure and composition in New Zealand native forests (Shaw 1983). While there have been no specific

studies of the spatial and temporal dynamics of dead wood availability in native forests, measured amounts of dead wood ranging from 0 – 550 Mg/ha in native forest plots suggests a patchily-distributed resource (Richardson et al. 2009). This patchily distributed resource supports the dominant paradigm that management aimed at conserving biodiversity should create a heterogeneous plantation landscape, thus reflecting conditions found in natural forests (Hartley 2002). Here, I have shown unique assemblages of saproxylic invertebrates associated with different dead wood ages. Therefore, management should seek to produce a range of deadwood age classes over forested landscapes. Because plantation forests have even aged stands this can only be achieved at a landscape scale with a mosaic of different ages and subsequent thinning and harvesting units. Future research needs to address how important the spatial arrangement and size of these heterogeneous compartments is for maintaining the processes which mediate community development of native biodiversity in plantation stands.

Moreover, other factors such as variation in dead wood species and dead wood types ,snags (standing dead wood) vs. stumps vs. logs vs. finer material, have been shown to be important in terms of saproxylic conservation (Hjältén et al. 2010){Bouget, 2011 #7992}. How these characteristics affect biodiversity can be incorporated into New Zealand plantations through management strategies such as ring barking selected trees (rather than felling them at thinning), planting different tree species and retention of larger diameter dead wood, warrants further investigation.

2.5 Appendices

Appendix 2.0. All taxonomic orders, Coleoptera species and Hymenoptera species with their maximum indicator value (indval) from the indicator species analysis, the age class (indcls) this applies too, the P-value (p-val) and the significance of this indicator value: "***" ≤ .001, "**" ≤ 0.01, "*" ≤ .05 and "." ≤ 0.1.The assigned feeding guild and origin (native or exotic) is given for Coleoptera species.

Indicator	indval	indcls	p-val	significance	Feeding group	Origin
Class/Order						
Thysanoptera	0.10	1	1.00			
Lepidoptera	0.28	1	0.51			
Coleoptera	0.32	1	0.02	*		
Isoptera	0.09	10	0.60			
Amphipoda	0.31	10	0.01	**		
Hymenoptera	0.35	10	0.07	.		
Psocoptera	0.14	2	0.30			
Annelida	0.04	4	0.90			
Blattodea	0.05	4	1.00			
Orthoptera	0.10	4	0.74			
Mollusca	0.21	4	0.15			
Chilopoda	0.26	4	0.06	.		
Acari	0.27	4	0.28			
Opiliones	0.15	6	0.26			
Dermaptera	0.19	6	0.19			
Diptera	0.23	6	0.67			
Collembola	0.28	6	0.25			
Hemiptera	0.38	6	0.00	**		
Araneae	0.43	6	0.00	**		
Platyhelminthes	0.07	8	0.86			
Pseudoscorpiones	0.24	8	0.06	.		
Diplopoda	0.26	8	0.39			
Isopoda	0.30	8	0.03	*		
Coleoptera						
Xenocnema spinipes	0.93	1	0.00	***	wood feeder	unknown
Brontopriscus pleuralis	0.07	1	0.80		wood feeder	unknown
Hylastes ater	0.07	1	1.00		wood feeder	exotic

Calliprason pallidum	0.09	1	1.00		wood feeder	native
Cryptamorpha brevicornis	0.20	1	0.15		fungal feeder	native
Bitoma insularis	0.30	1	0.03	*	wood feeder	unknown
Hylurgus ligniperda	0.30	1	0.03	*	wood feeder	exotic
Arthrolips oblonga	0.50	1	0.00	***	fungal feeder	native
Sapintus pellucidipes	0.14	2	0.23		scavenger	unknown
Sepedophilus sp. 89	0.22	2	0.03	*	predator or parasitoid	unknown
Cis sp. 11	0.25	2	0.02	*	wood feeder	native
Pachycotes peregrinus	0.27	2	0.06		wood feeder	unknown
Crisius binotatus	0.30	2	0.01	*	wood feeder	unknown
Elateridae sp. 48	0.03	4	1.00		wood feeder	unknown
Maorothius sp.78	0.05	4	1.00		predator or parasitoid	unknown
Kupeus arcuatus	0.05	4	0.85		fungal feeder	unknown
Omaliinae sp. 63	0.07	4	0.87		unknown	unknown
Archaeoglenes costipennis	0.08	4	0.81		unknown	unknown
Aleocharinae sp. 88	0.09	4	0.62		predator or parasitoid	unknown
Cis sp. 13	0.10	4	1.00		wood feeder	native
Agyrtodes sp. 15	0.20	4	0.07	.	fungal feeder	unknown
Parepierus sp. 5	0.21	4	0.15		predator or parasitoid	native
Mitrastethus baridioides	0.22	4	0.07		wood feeder	unknown
Euplectinae sp. 77	0.23	4	0.07	.	predator or parasitoid	unknown
Brachynopus scutellaris	0.25	4	0.03	*	predator or parasitoid	unknown
Philothermus sp. 44	0.34	4	0.01	**	fungal feeder	unknown
Menimus sp. 7	0.07	6	0.87		fungal feeder	native

Scaphisoma funereum	0.07	6	0.86		predator or parasitoid	unknown
Aleocharinae sp. 65	0.08	6	0.72		unknown	unknown
Ptinella sp. 61	0.10	6	1.00		unknown	unknown
Sagola sp. 74	0.12	6	0.36		predator or parasitoid	unknown
Dryocora howitti	0.12	6	0.37		unknown	native
Xantholinini sp. 69	0.12	6	0.61		unknown	unknown
Cossoninae sp. 21	0.13	6	0.40		wood feeder	unknown
Euplectinae sp. 75	0.14	6	0.24		predator or parasitoid	unknown
Xantholinini sp. 79	0.20	6	0.17		predator or parasitoid	unknown
Prionoplus reticularis	0.21	6	0.07	.	wood feeder	native
Micro-Staphylinidae	0.28	6	0.09	.	predator or parasitoid	unknown
Sepedophilus sp. 90	0.06	8	0.80		predator or parasitoid	unknown
Synorthus sp. 39	0.07	8	0.87		unknown	unknown
Eupines sp. 73	0.08	8	0.87		predator or parasitoid	unknown
Sericotrogus subaenescens	0.10	8	0.50		wood feeder	unknown
Protelater sp. 45	0.15	8	0.16		wood feeder	unknown
Paratorchus sp. 83	0.15	8	0.12		predator or parasitoid	unknown
Kiwitachys antarcticus	0.17	8	0.13		predator or parasitoid	unknown
Paederinae sp. 84	0.20	8	0.14		predator or parasitoid	unknown
Uloma tenebrionoides	0.21	8	0.18		wood feeder	native
Kaveinga bellorum	0.26	8	0.05	.	fungal feeder	unknown
Aleocharinae sp. 94	0.27	8	0.08		unknown	unknown
Scydmaeninae sp. 6	0.28	8	0.02	*	predator or parasitoid	unknown
Neopelatopini n.g n.sp. 14	0.29	8	0.05	.	fungal feeder	native

Cryptorhynchinae sp. 24	0.29	8	0.02	*	wood feeder	unknown
Ptinella propria	0.32	8	0.01	*	fungal feeder	unknown
Phrynixus sp. 23	0.36	8	0.00	**	wood feeder	unknown
Sagola sp. 71	0.37	8	0.01	*	predator or parasitoid	unknown
Neopelatopini n.g n.sp. 38	0.08	10	0.88		scavenger	unknown
Paromalia vestita	0.10	10	1.00		wood feeder	unknown
Sepedophilus sp. 92	0.12	10	0.32		predator or parasitoid	unknown
Euplectitae sp. 76	0.20	10	0.14		predator or parasitoid	unknown
Hyperomma sp. 80	0.22	10	0.06	.	predator or parasitoid	unknown
Hymenoptera Species						
Mymaridae sp. 24	0.20	1	0.529			
Pteromalidae sp. 13	0.38	1	0.012	*		
Ochetellus glaber	0.11	4	0.799			
Tersilochinae GenusB sp. Co 1	0.11	4	0.788			
Rhyssalinae-*Metaspathius* sp. 17	0.13	4	0.384			
Strumigenys perplexa	0.16	4	0.29			
Tersilochinae-GenusB sp. Au2	0.22	4	0.201			
Diapriidae sp. 23	0.30	4	0.214			
Alyssinae-*Dinotrema philipi*	0.11	6	0.798			
Discothyrea Antarctica	0.22	6	0.108			
Platygastridae sp. 8	0.42	6	0.003	**		
Proctotrupidae-Genus6	0.08	8	0.785			
Monomorium antarcticum	0.19	8	0.435			
Hypoponera eduardi	0.06	10	0.755			
Oxyserphus sp. 3	0.16	10	0.282			
Pachycondyla castanea	0.35	10	0.05	*		
Amblyopone australis	0.46	10	0.019	*		

Chapter 3 Local and landscape scale effects on saproxylic invertebrates – effects of deadwood species and native forest proximity in a plantation forest landscape

3.1 Introduction

Habitat loss and fragmentation (the breaking apart of habitat) are critical agents of species decline (Sala et al. 2000, Fahrig 2003, Ewers and Didham 2006). The effects of fragmentation on individual species are strongly mediated by the degree to which matrix quality influences dispersal rates, the magnitude and extent of edge effects, and the provision of external resource subsidies from adjacent habitat (Ewers and Didham 2006). Such edge effects can be mitigated where native forest fragments are surrounded by plantation forests, for example buffering remnants against external microclimate influences (Denyer et al. 2006). The response of species to habitat edges may be mediated by interactions with other organisms such as predators (Wimp et al. 2011) or plant resource distributions (Blackburn et al. 2011). Saproxylic beetle assemblages respond strongly to coarse woody debris abundance and canopy openness (Müller et al. 2010) and are more often associated with gaps created by bark beetles (which have high amounts of deadwood) than meadows (Müller et al. 2008). Open plantations have similarly high levels of residual deadwood after harvesting which may provide a resource subsidy for saproxylic invertebrates. Although plantations do not support the same biodiversity as natural forests (Barlow et al. 2007), they can provide surrogate habitat for a range of native species, including threatened taxa (Norton 1996, Pawson et al. 2008, Pawson et al. 2010).

Northern Hemisphere studies have shown that many saproxylic taxa can be substrate specific, and that different tree species often support a subset of the total saproxylic community

(Lindhe and Lindelow 2004, Lindbladh et al. 2007). Thus, in an intensely managed monoculture, such as *P. radiata* plantations one would expect to find a depauperate saproxylic community. Almost 90% of New Zealand's production forests are composed of even aged stands of *Pinus radiata*, an exotic conifer, (Anon 2010). Stands are harvested by clearfelling between the ages of 26 to 32 years depending on the growing region, and a large amount of deadwood, derived from harvesting, pruning and thinning operations, is present at certain periods throughout the rotation. However, such plantations are not strictly monocultures as they support a diverse under-storey of native plant species, including many woody and herbaceous species (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003). In addition to the within stand flora, New Zealand plantations often include reserves of native habitat embedded between production stands (Brockerhoff et al. 2008a, Langer et al. 2008). This greater floristic diversity in such native remnants is likely to result in a greater faunal diversity as well (Lindenmayer and Hobbs 2004).

The availability of, and to a lesser extent the proximity to, native habitat remnants within the landscape are key determinants of species survival (Hodgson et al. 2011). However, given the high levels of native forest loss in New Zealand (Brockerhoff et al. 2008b), and the host specificity of many saproxylic invertebrates (Lindhe and Lindelöw 2004, Lindbladh et al. 2007, Jie et al. 2008), native understory woody species in plantations could be important for maintaining saproxylic invertebrates in fragmented landscapes. In New Zealand plantations, proximity to native habitat is known to be an important factor determining the community composition of other insects, such as ground beetles (Pawson et al. 2008). As such it is likely that proximity to native remnants will influence the relationship between woody understory diversity and saproxylic species diversity within intensely managed plantation forests.

Previous studies of saproxylic beetles have concentrated on assessing changes in community composition as a function of deadwood age and wood species (Lindhe and Lindelow 2004, Persiani et al. 2010). Some have extended this further to examine other environmental factors that may determine saproxylic community composition, such as habitat associations, wood postures, and spatio-temporal patterns (Ulyshen et al. 2004, Lindbladh et al. 2007, Jie et al. 2008), while others have studied the changes across forest edges (Müller et al. 2008).

I aim to quantify how resource availability (different wood species) and proximity to native habitat influence the structure of saproxylic invertebrate communities (richness and composition) in managed plantation forests. It is likely that communities of saproxylic invertebrates in different habitat types (native remnants, habitat boundaries and production stands) will have unique communities of species due to habitat specialisation. However, mixing of species at forest-boundaries may increase species richness at these sites. In terms of wood species I expected overall species richness would be highest in *P. radiata* as this is the dominant dead wood resource and there should be a large pool of potential colonists in these landscapes. I expect unique assemblages to colonise different species of dead wood because of widely reported host specificity of many species (Lindhe and Lindelöw 2004, Lindbladh et al. 2007, Jie et al. 2008). It is likely that such host specificity will be consistent across sample transects because many invertebrates in plantations are known to be disturbance adapted with good dispersal abilities (Pawson et al. 2009, Pawson et al. 2012).

To my knowledge this is the first study to test both the importance of resource availability supplied understory tree diversity at maintaining saproxylic invertebrates in plantations and how this is mediated by edge effects created by the proximity to native remnants on the saproxylic community in a managed forest landscape.

3.2 Methods

3.2.1 Site selection

Spatial data on plantation forest attributes were supplied by participating forest management companies and the area of native forest cover was extracted from the New Zealand Landcover Database (LCDB2) (Terralink 2004a). All GIS analyses were conducted in Arc Map 9.3.1 (ESRI, Redlands, USA). A GIS script was then used to calculate the proportion of native habitat within a 2km radius of each point on a 100 m grid laid across the boundary between any native forest cover and plantation forest landcover type. Points were selected from this grid that straddled the boundary between native and pine forest within the Tarawera plantation forest (situated within the larger study region described in Chapter 2) that had less than 20 percent cover of native forest in the surrounding 2km radius. Standardising by the proportion of native habitat was done to avoid confounding the effect of habitat size and edge effects. From these points nine study landscapes with young pine (planted between 2007 and 2008) were selected and visited to assess their suitability in terms of access and to ground truth the accuracy of the available GIS data. Once chosen I established a standardised transect at each of three landscapes to sample saproxylic invertebrates across the native forest-plantation boundary. I collected samples at seven distances from the edge (-125(native), -25, -5, 0 (edge), +5, +25, +125 (pine) metres) (Figure 3.1).

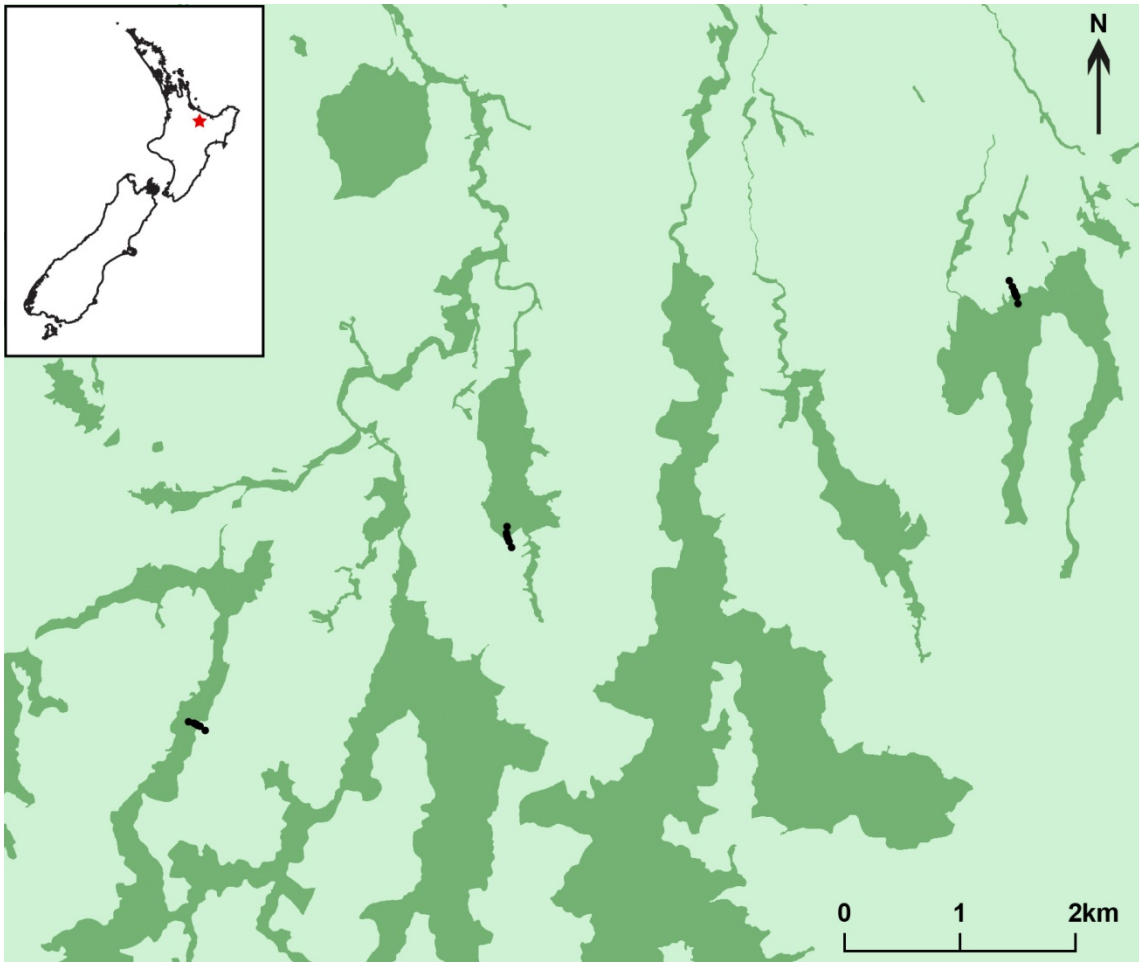


Figure 3.1 Study sites (circles) located at the boundary between native remnants (dark green) and plantation forest (light green) stands within the Tarawera forest. Study area location within insert of New Zealand coastline is indicated with star symbol.

3.2.2 Invertebrate sampling

To sample saproxylic invertebrates I used experimental log billets. Billets are short sections of wood placed at each distance on the transect and act as passive 'traps' that are colonised by deadwood feeding invertebrates (Hammond 1997). A total of three billet logs of each wood species were placed at each distance with an additional three *Pinus radiata* billet logs which were part of another research trial quantifying the effect of invertebrate community composition on wood decomposition rates (Figure 3.2). *Pinus radiata* billets were placed in the forest on the 12th and 13th October 2009 and were removed from the forest on the 18th and 19th February 2010. Native billets were placed in the forest on the 23rd October 2009 and removed on 27th February 2010. Billets were transferred to rearing chambers within 24 hours after removal from the forest (see chapter 2.2.4). Each *P. radiata* billet was placed in an individual rearing bag, while the three billets from each of the three native tree species; *Melicytus ramiflorus*, *Schefflera digitata* and *Aristotelia serrata*, were pooled inside one emergence bag. Billets were left in the rearing chambers for six months.

All billet logs were 30 cm in length and were collected from live trees within Tarawera forest. *P. radiata* billet logs were taken from trees with an approximate diameter at breast height (DBH) of 15 cm. *Melicytus ramiflorus, S. digitata* and *A. serrata* were taken from live trees in the understory of mature plantation stands in the Tarawera plantation. Given the constraint of a ~28 year rotation length the understory trees do not reach maturity and thus the diameter of available native trees was more limited. For native wood species I selected trees with a DBH of 10cm. Because the native billets are smaller in diameter than the pine billets, three billets of each native species were pooled in one emergence bag, while the three pseudo-replicate *P. radiata* billets were bagged separately and for all analysis the samples from one randomly drawn *P. radiata* billet was used. This approach was taken so that

samples compared were reared from a similar volume of wood, 4083 (±285) for *P. radiata*, 4962cm^3 (±298cm^3) for *S. digitata*, 4203cm^3 (±203cm^3) for *M. ramiflorus* and 3707 cm^3 (±307cm^3) for *A. serrata*. To eliminate the potential confounding effect of small differences in volume and sampling effort, I took a conservative approach and included volume as a covariable in multivariate analyses (ordinations) and used mixed effects models with volume as the first term in every model to compare wood species effects on abundance and diversity of invertebrates. While this controls for the effect of wood volume it cannot control for the potential effect of the extra *P. radiata* billet logs which were not used in analysis giving off volatiles which may have attracted more invertebrates to this wood type.

The sub-canopy trees *M. ramiflorus*, *S. digitata* and *A. serrata* were selected because they occur frequently in mature *P. radiata* stands in the region (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003). In addition, they are all common components of both native lowland forest patches in the eastern Bay of Plenty and throughout New Zealand (Nicholls 1991, Dawson and Lucus 2005). All three tree species grow to approximately 10 m in height. *M. ramiflorus* and *S. digitata* have smooth, soft and fragile bark, whereas *A. serrata* has smooth bark with corky stripes (Dawson and Lucus 2005). These bark characteristics contrast significantly with *P. radiata* which has harder, thicker and deeply furrowed bark with scaly ridges. Deadwood of all three native species is readily available in young pine stands after harvesting. However, as stands regenerate and the deadwood resource decomposes the availability of the resource decreases in plantation stands compared to native fragments.

Figure 3.2. Three experimental wood billets of each native tree species; *M. ramiflorus*, *S. digitata* and *A. serrata*, alongside six *P. radiata* wood billets (foreground).

3.2.3 Insect identification

Rearing saproxylic invertebrates from different wood resources is advantageous as I am able to distinguish the invertebrate communities associated with each species of deadwood, which could not be achieved with other sampling methods, such as flight intercept traps. Samples were initially sorted to invertebrate classes and orders and stored in 70% ethanol for future analysis. Selected orders (Diptera, Coleoptera, Hymenoptera (Formicidae), Hymenoptera (other), Diplopoda and Hemiptera) were stored in separate vials as they are of interest to specific researchers and in future may be sorted to a finer taxonomic resolution. Remaining classes and orders were removed and stored together in a single vial, except Collembola and Acari which were counted and left in the remaining 'by catch'. Coleoptera adults were identified to morpho-species with representative specimens pinned for each species. A reference collection is housed at the Scion, Ilam Office. All ordinal and beetle morphospecies were checked by an experienced entomologist (Stephen Pawson, Scion). Where possible species names were assigned to Coleoptera and checked by Stephen Pawson. Hymenoptera

were identified to morphospecies and where possible species names were assigned by Darren Ward (Landcare Research). In total, only 348 specimens of Hymenoptera emerged and there was insufficient replication to undertake a meaningful community-level analysis for this group so they were not examined further.

3.2.4 Environmental covariables

All study sites were visited between 12 and 15 March 2010 and Litter abundance, dead wood abundance, site moisture and slope were measured on a subjective scale (Table 3.1) and aspect was measured with a handheld compass. Because this date was after the billets where removed and these measures were not repeated temporally, only variables which do not change over short temporal scales were measured. Environmental co-variables that may influence patterns in invertebrate community structure were also extracted from geospatial data layers using Arc Map 9.3.1 (ESRI, Redlands, USA). Mean annual temperature data were extracted from the underlying Land Environments of New Zealand data layers (Leathwick et al. 2002). Artificial shade was supplied to very dry sites with no natural shade using stacked *P. radiata* dead wood material, this material was very dry and unlikely to contain any invertebrates that may colonise the billets and bias the results. However, this was also used as a covariable in analysis of community composition to avoid any bias it may have created. A full list of environmental variables is given in Table 3.2.

Table 3.1 Scoring systems used to provide a qualitative measure of dead wood abundance, litter abundance, moisture and slope surrounding each trapping site. Qualitative scale for dead wood abundance, litter abundance and moisture is after Pawson (2006).

Score	Dead-wood abundance	Litter abundance	Moisture	Slope
1	None or very little (at most a few twigs)	Little (0 - 5% cover)	Poor drainage (surface water is present even during prolonged dry spells)	Flat (level terrain, easy walking)
2	Intermediate	Intermediate	Intermediate	Intermediate
3	Medium (at least one log > 10cm diameter)	Medium (30 - 50% litter cover)	Medium drainage (at least one spot gives way under foot)	Medium (travel is difficult when wet)
4	Intermediate	Intermediate	Intermediate	Intermediate
5	Abundant deadwood (movement is impeded by dead wood)	Abundant (70% or more cover of thick litter)	Well drained (no surface water even during prolonged rain)	Steep (travel is difficult in all conditions and extreme caution is required when wet)

Table 3.2. Description of environmental variables and units of measurement used in multivariate community analyses.

Variable	Explanation	Unit of measure
Proximity	Distance from the edge of plantation and native forest fragments (-125m (native forest) to 125 m (plantation forest))	Metres
Dead wood abundance	Five point scale used to classify dead wood abundance within a 5 m radius of wood billets	Categorical
Litter abundance	Five point scale used to classify litter abundance within a 5 m radius of wood billets	Categorical
Moisture	Five point scale used to classify soil moisture within a 5 m radius of wood billets	Categorical
Aspect	The aspect of the individual sites measured with a handheld compass	Degrees from North
Slope	Five point scale used to classify the slope of the site*	Categorical
Latitude	Latitudinal distance from centroid of all study sites	Metres
Longitude	Longitudinal distance from centroid of all study sites	Metres
Native 5000	Proportion of native habitat within a 5000m radius	Proportion
Native 2000	Proportion of native habitat within a 2000m radius	Proportion
Native 1000	Proportion of native habitat within a 1000m radius	Proportion
Native 500	Proportion of native habitat within a 500m radius	Proportion
Native 200	Proportion of native habitat within a 200m radius	Proportion
Native 100	Proportion of native habitat within a 100m radius	Proportion
Pine age	The time in years since plantation stand establishment	Years
Volume	The volume of dead wood the invertebrate sample was reared from	Cubic Metres
Mean annual temperature	Mean annual temperature of the site	℃
Dead wood species	*Pinus radiata, Schefflera digitata, Melicytus ramiflorus* or *Aristotelia serrata.*	Categorical
Proximity * wood species	An interaction term for dead wood species and proximity interaction	Categorical
Landscape	One of three edge gradients where study sites were located	Categorical
Artificial shade	Whether or not artificial shade was applied at site	Binary

3.2.5 Data analysis

Richness and abundance

To test for an effect of wood species and proximity to interior native forest and their interaction on order group and Coleoptera species abundance I used a backwards elimination procedure. The initial model contained volume of wood the sample emerged from (to control for differences in volume) and the main treatments; proximity as a continuous predictor and wood species (categorical) with their interaction term last in the model. I used linear mixed effects models with landscape as a random factor, insignificant interaction terms and main effects were dropped and the reduced most simplified parsimonious model was used to test the effect of wood species and proximity to native habitat if they were not removed. The selected models included wood species and proximity to native habitat as the interaction was insignificant and I tested the main effects of these terms by entering them last in the model after volume. I used a similar approach to test for an effect of wood species and proximity and their interaction on order group and Coleoptera species richness (total number of species or groups), except abundance of individuals was put at the start of the model to control for abundance effects on richness and give a more rigorous test of species richness. The selection procedure resulted in only abundance and volume being retained to test the effect of proximity to native habitat on order group richness as wood species did not have a significant main effect or interaction with proximity and was removed from the model. Only abundance, volume and wood species were retained in the model to test the drivers of Coleoptera species richness as proximity and it's interaction with wood species were insignificant. All models were run in R with the package *nlme*.

For a rigorous comparison of species density across the different wood species sample based rarefaction was conducted using the analytical approach of Colwell et al. (2004). Rarefaction results were subsequently rescaled to produce expected species accumulation curves based on the number of individuals, as recommended by Gotelli and Colwell (2001). To compare expected species richness between different wood types a cubic polynomial function was fitted to each species accumulation curve and subsequently evaluated at the highest equivalent number of individuals present in each data set (Invertebrate orders, Coleoptera species) to provide a point of comparison. All order group and species rarefaction analyses were calculated using Estimate S, version 8.2.0 (Colwell 2006).

Community Composition

Prior to analysis of taxonomic group and Coleoptera community structure those species and samples with abundance of 2 or less were removed to down weight the influence of rare species in the analysis. Community composition analyses were conducted in a step wise process, as suggested by Anderson and Willis (2003). An initial unconstrained non-metric Multidimensional Scaling (MDS) ordination was conducted in R with the function *metaMDS* from the vegan 1.15-3 package. This function allows the user to select the number of dimensions (K) to be analysed. There are no set selection criteria for choosing appropriate values of K (Anderson and Willis 2003). The analysis was run repeatedly on the two data sets (invertebrate orders and Coleoptera species) using Bray-Curtis dissimilarities with sequentially higher levels of K, until the reduction in stress with increasing levels of K was small (Legendre and Legendre 1998). This approach has been applied by plotting stress as a function of the number of dimensions rather than a "rule of thumb approach" as was applied in chapter 2 (these plots are given in Appendix 3.2). Once

the model with the appropriate K level was determined the *envfit* command from the vegan 1.15-3 package was used to assess the correlation of environmental variables to the selected NMDS model using 999 permutations of the environmental variables. The significant variables of interest were then used in a constrained analysis of principal coordinates (CAP) with significant variables that were not of interest partialled out using the *condition* command in the *capscale* function of R's vegan 1.15-3 package (*envfit* results and *capscale* models are given in Appendix 3.3 A and B). These environmental variables were tested for co-linearity and variables which had correlation of over 0.90 were combined and represented by the variable which explained the most variation in the NMDS sample scores. Environmental variables used in CAP models were then fitted to the CAP site scores to determine which environmental variables had significant associations with community composition after partialling out potentially autocorrelated variables.

Fitting edge functions

To explore how order group and Coleoptera species abundance, richness and community composition varied continuously across the habitat edges for each wood type I used the edge fitting functions of Ewers and Didham (2006), which does not assume linearity and thereby provides a more accurate test of the variation in richness along sampling transects. This procedure chooses the best fit model to describe a change in a continuous response variable based on AIC scores from four models of increasing complexity from the simplest null model of no change across the sample transect. This approach allowed me to visualise patterns in the community composition based on the axis scores (I used CAP axis 1) of samples. This approach also allowed a more rigorous test of variation in abundance and richness across the sampling transects but I was not able to control for the confounding effects of volume on abundance, or volume and abundance on richness. However, the

results are still relevant because of the standardised sampling design from similar volumes of wood and while species richness may be an artefact of abundance this is still biologically meaningful.

Identification of individual species responses

Invertebrate orders and Coleoptera species were tested for associations with specific dead wood species and habitat types (native forest, edge and plantation forest) using the indicator value (*IndVal*) approach of Dufrêne and Legendre (1997). Indicator values are a robust and quantitative method of identifying species that are characteristic of a particular treatment group that is chosen a-priori. All indicator value analyses were conducted using the R labdsv 1.4-1 package (Roberts 2010).

3.3 Results

3.3.1 Species and taxonomic group richness

A total of 12 864 individuals were extracted and sorted to taxonomic class and order from 210 log billets that were grouped into 84 emergence-bag samples. Across all four wood species invertebrates were sorted into 15 taxonomic groups (Table 3.2) and the 1202 adult Coleoptera were sorted to 61 morphospecies. Almost twice as many individuals (6514) emerged from the *P. radiata* samples compared to the *S. digitata* samples (3504) and four times as many invertebrates emerged from the *P. radiata* samples than that from the *M. ramiflorus* and *A. serrata* samples (1244 and 1602 respectively). The most abundant taxa across all wood types were Diptera, Coleoptera, and Collembola. In total these three groups represented 12 292 specimens, or 96% of the total catch.

Table 3.3 Total number of invertebrates emerging from *Pinus radiata*, *Schleffera digitata*, *Melicytus ramiflorus* and *Aristotelia serrata*.

Invertebrate order	*Pinus radiata*	*Schefflera digitata*	*Melicytus ramiflorus*	*Aristotelia serrata*	Total
Annelida	10	0	0	0	10
Isopoda	0	0	0	6	6
Collembola	697	875	667	383	2622
Diptera	4079	1772	337	930	7118
Coleoptera (including larvae)	1429	740	165	218	2552
Hymenoptera (other/wasps)	127	13	7	5	152
Lepidoptera	31	23	24	9	87
Hemiptera	7	5	6	6	24
Hymenoptera (Formicidae)	0	0	0	7	7
Dermaptera	3	0	0	1	4
Chilopoda	5	11	7	3	26
Diplopoda	18	1	2	3	24
Acari	103	58	27	26	214
Pseudoscorpiones	1	6	0	3	10
Aranae	4	0	2	2	8
Total	6514	3504	1244	1602	12864

3.3.2 Linear effects of wood species and native habitat proximity

The interaction between wood species and proximity to native habitat on total invertebrate abundance was insignificant ($F_{3,79} = 1.93$, $P = 0.13$). This term was dropped from the model and the simplified model with volume, proximity and wood species showed there was a significant decrease in total invertebrate abundance as proximity from native habitat increased ($F_{1,81} = 22.50$, $P < 0.0001$) and wood species ($F_{3,79} = 10.61$, $P < 0.0001$) also had a significant effect on invertebrate. The interaction between wood species and proximity to native habitat on Coleoptera abundance was also insignificant ($F_{3,79} = 0.31$, $P = 0.8145$). This term was dropped from the model and the simplified model with volume, proximity and wood species showed there was a significant decrease in Coleoptera abundance as

proximity to native habitat increased ($F_{1,81}$ = 33.90, P < 0.0001) and wood species ($F_{3,79}$ = 15.18, P < 0.0001) also had a significant effect on Coleoptera abundance.

The interaction between wood species and proximity to native habitat on order richness was insignificant ($F_{3,79}$ = 1.43, P = 0.24) and so was the effect of wood species ($F_{3,79}$ = , P<0.13). These terms were dropped from the model and the simplified model with volume and abundance showed proximity to native habitat had a significant effect on order richness ($F_{1,81}$ = 4.3231, P = 0.04). The interaction between wood species and proximity to native habitat on Coleoptera species richness was also insignificant (F3,79 = 1.24, P=0.30) and so was the effect of proximity to native habitat ($F_{1,81}$ = 3.808, P = 0.06). These terms were dropped from the model and the simplified model with volume and abundance showed wood species had a significant effect on Coleoptera species richness ($F_{3,79}$ = 5.35, P = 0.002). A more conservative approach to comparing the effect of wood species on class/order group and Coleoptera species richness is rarefaction standardised for the highest common sample size. This provides a measure of species density rather than number, which may be correlated with abundance. Rarefied richness showed that there were no significant differences in taxonomic class/order or Coleoptera species richness with wood type (Figure 3.3).

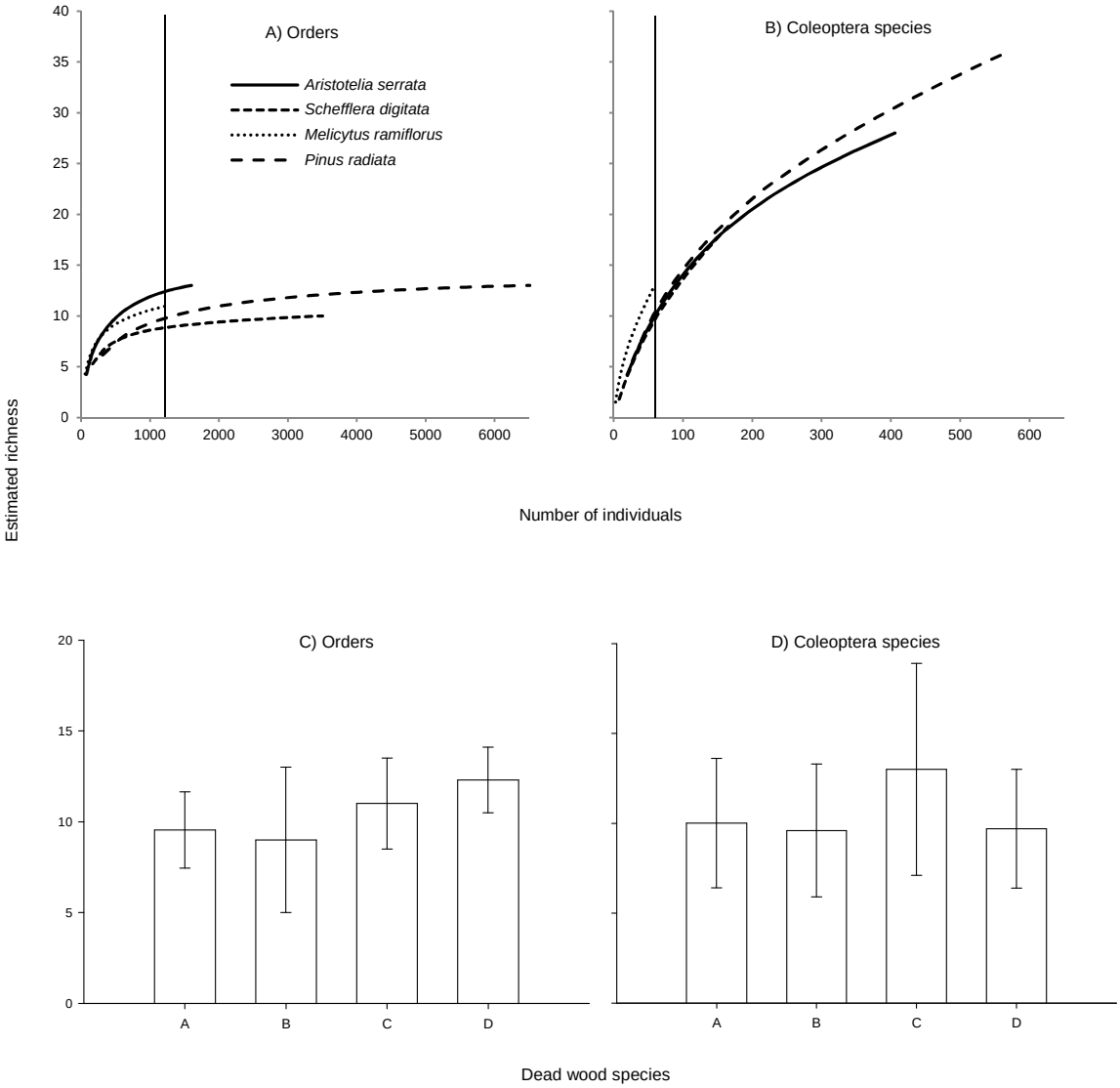


Figure 3.3 Comparison of sample-based richness accumulation curves for samples pooled by different wood species, for (A) taxonomic classes and orders. and (B) Coleoptera species. The comparison at the indicated line on the accumulation curves is indicated for (C) taxonomic classes and orders (1244 individuals), and (D) Coleoptera species (59 individuals) with error bars indicating 95% confidence intervals. In panel C and D characters on X-axis represent *Pinus radiata* (A), *Schefflerra digitata* (B), *Melicytus ramiflorus* (C) and *Aristotelia serrata* (D).

3.3.3 Community composition

Class/Ordinal

Removal of empty samples resulted in a data set that consisted of 12 864 invertebrates in 15 taxonomic classes and orders from 83 samples. An unconstrained NMDS showed that there was high variance in the invertebrate ordinal community composition and considerable overlap between the different wood species and habitat types (Figure 3.4 A). Fitting environmental variables to the NMDS showed that shade and the interaction term for proximity and wood species were significant predictors of invertebrate community composition while wood species and proximity, as well as all other environmental variables did not have a significant effect on the distribution of samples in the ordination space (Full results in Appendix 3.2 A).

After constraining by all significant environmental predictors and partialling out confounding effects (Shade, for full CAP formula see Appendix 3.2 B) the native forest proximity by wood species interaction was a significant predictor of invertebrate order (Table 3.5). This is indicated by the fitted vector which explains 51% of the variation in invertebrate order composition (Figure 3.5: A and Table 3.5). This was the only constraining variable that was significant and suggests that the effect of deadwood species identity on taxonomic class/order composition is not consistent at all distances from native forest. This effect is not clearly visualised on the biplot diagram because of the extensive overlap of samples from different wood species and habitat types (Figure 3.5: A).

Coleoptera

Removal of rare species and samples with no individuals resulted in a data set that consisted of 1168 Coleoptera individuals and 47 species from 71 samples. An unconstrained NMDS

showed that despite high variance in Coleoptera community composition with distinct differences between different wood species indicated by wood species centroids (Figures 3.5 B). The *P. radiata* billets had the most distinct community composition and exhibited a degree of separation between samples in plantation forest and native forest habitat types (Figure 3.4 B). Fitting environmental variables to the NMDS showed that dead wood species explained the most variation in Coleoptera community composition followed by proximity to native habitat and these two variables were the only two constraining variables used for CAP ordination (Appendix 3.2 A and B). Longitude, latitude, Native 5000, Native 1000, and MAT were also significant predictors of community composition. These variables were intercorrelated and were combined into one variable represented by longitude that was the best predictor of variation in Coleoptera community composition. Shade also explained a significant proportion of variation in Coleoptera community composition and was partialled out along with the confounding variable latitude in the CAP ordination (Appendix 3.2 A and B). While some measured landscape variables (proximity, longitude, latitude, native 5000 and native 1000) were significant predictors of Coleoptera community composition, none of the subjectively measured site variables (dead wood abundance, moisture and litter abundance) were significant predictors of Coleoptera community composition.

Constraining the ordination by significant environmental predictors (dead wood species, proximity and their interaction) and partialling out the effects of unwanted effects of covariables (Shade and longitude (longitude = latitude, Native 5000, Native 1000, and MAT), for full formula see Appendix 3.2 B) showed that deadwood species was a strong predictor of Coleoptera species composition (Table 3.5). This is reflected in the distribution of wood species centroids in the CAP biplot which shows *P. radiata* has a distinct saproxylic beetle composition to that of all the native woods (Figure 3.5 B). All the *A. serrata* native forest site

samples except one also form a unique cluster (Figure 3.5 B). The proximity of the site to interior native forest was only marginally significant (P = 0.053) predictor of Coleoptera community composition (Table 3.5), however unlike ordinal community composition there was no interaction effect between proximity and deadwood species identity.

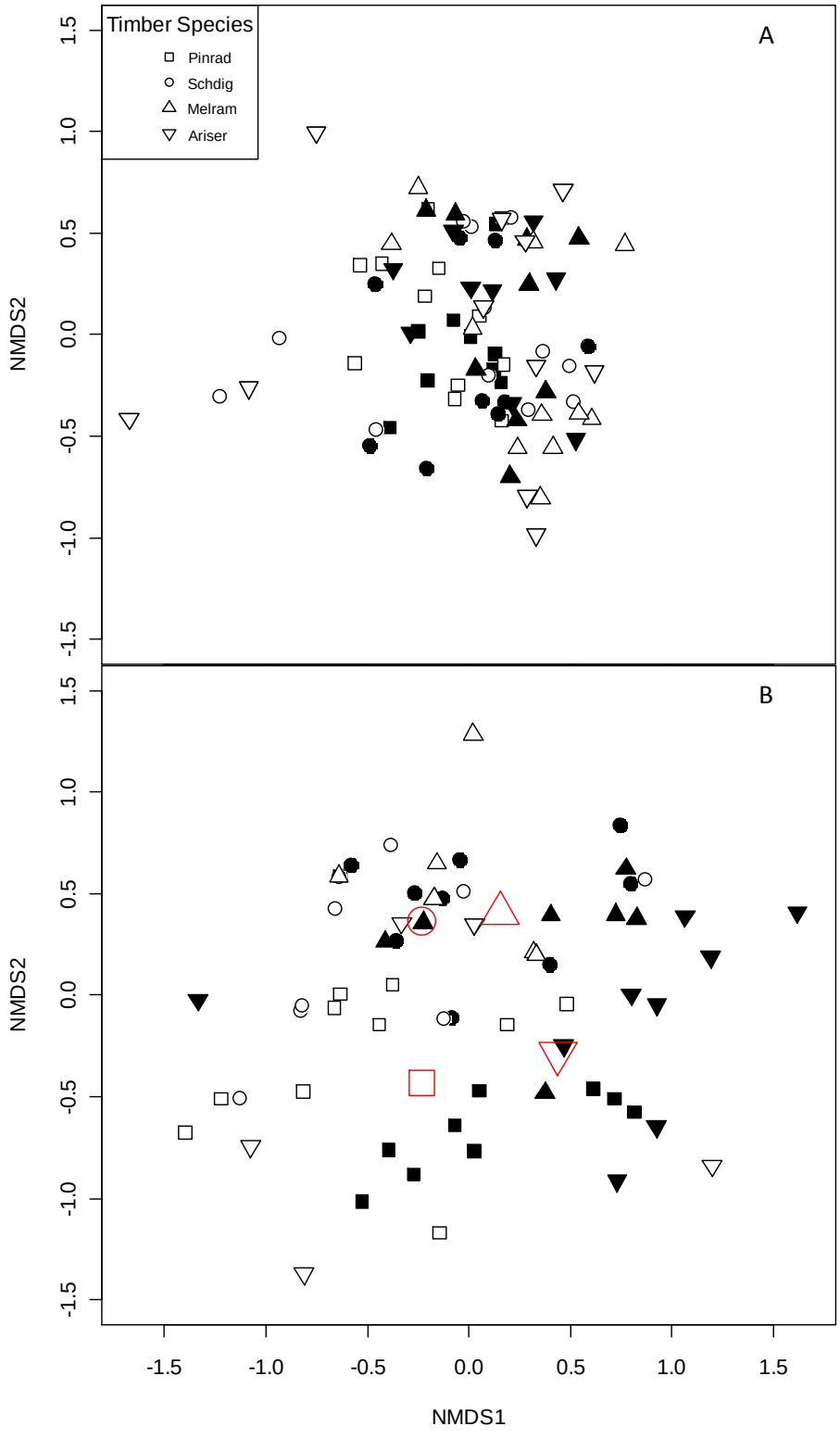


Figure 3.4 Community composition of different dead wood species (Pinrad = *P.radiata*, Schdig = *S. digitata*, Melram = *M. ramiflorus* and Ariser = *A. serrata*) visualised using unconstrained NMDS plots of the first two axis ; A) invertebrate orders (K= 5 dimensions, stress = 12.86) and B) Coleoptera species (K = 4 dimensions, stress = 13.06) for plantation (including edge sites; hollow symbols) and

native habitat (filled symbols). Large symbols represent group centroids for wood species (plot B only).

Table 3.4: Constraining variables that were significant predictors of invertebrate ordinal and Coleoptera species composition after a partial CAP.

	Invertebrate orders			Coleoptera species		
Variable	r2	Pr(>r)	Significance	r2	Pr(>r)	Significance
Proximity				0.08	0.053	.
Dead wood species				0.64	0.001	***
Proximity*wood species	0.51	0.001	***			

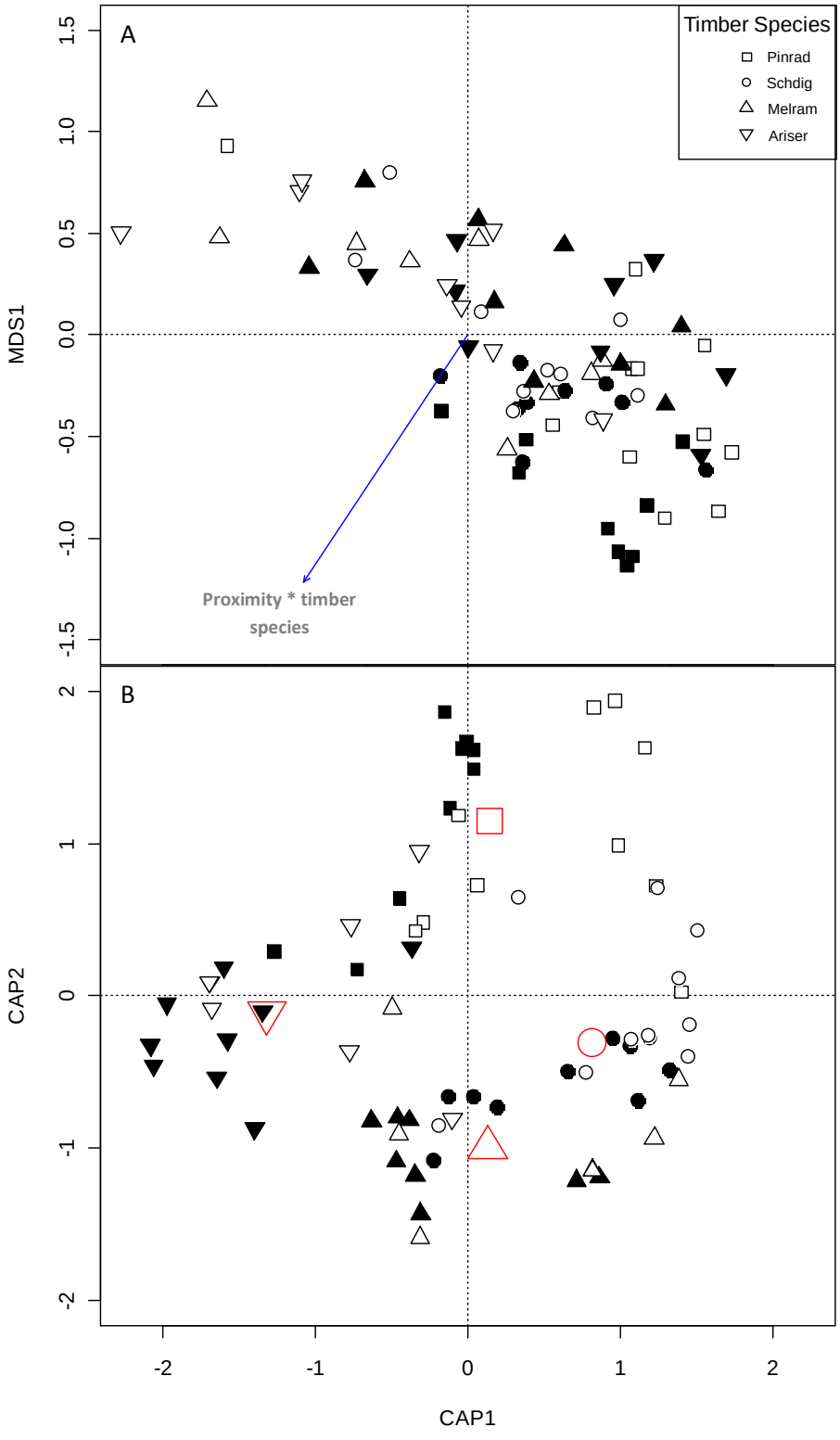


Figure 3.5 Community composition of different dead wood species (Pinrad = *P.radiata*, Schdig = *S. digitata*, Melram = *M. ramiflorus* and Ariser = *A. serrata*) visualised with plots of first two axis of Canonical Analysis of Principle Coordinates with significant environmental vectors for A) invertebrate orders (note there was only one constrained axis) and B) Coleoptera species for

plantation (including edge sites; hollow symbols) and native habitat (filled symbols). Large symbols represent group centroids for wood species (plot B only).

3.3.4 Edge response functions

Aristotelia serrata was the only wood species which showed a significant change in the abundance of total invertebrates captured across the native-plantation forest boundary with more invertebrates reared from this wood type when it was in the native forest compared to plantation forest sites (Figure3.7 A). The abundance of Coleoptera was higher in billets situated in native forest as opposed to plantation sites for all wood species except *S. digitata*. *Pinus radiata* had the highest abundance of Coleoptera of all deadwood species sampled in native forest. The abundance of Coleoptera in *P. radiata* wood declined with the transition from native to plantation forest where Coleoptera abundance was similar to that of the three native wood species (Figure 3.6 B).

The richness of taxonomic order groups did not change across the sample transects for *P. radiata* dead wood or that of *A. serrata* (Figure 3.6 C). A greater number of taxonomic orders were present in *Melicytus ramiflorus* and *S. digitata* had placed in native forest habitat as opposed to plantation habitat (Figure 3.6 C). In contrast to the response of taxonomic orders in *P. radiata* wood the number of Coleoptera species found in *P. radiata* wood decreased linearly with increasing distance from sites 125 m inside native forest (Figure 3.6 D). The number of Coleoptera species which colonise the native wood species *A. serrata* and *M. ramiflorus* also decreased with increasing distance from native forest but their response was logistic and showed the greatest decrease in close distance to the edge of plantation forest and native forest habitat (Figure 3.6 D). No change with respect to distance from native forest was detected in the number of Coleoptera species which colonise *S. digitata* wood billets (Figure 3.6 D).

Plotting the taxonomic order community composition for the different wood species as a function of proximity to native habitat showed no overall trend in community composition with respect to distance from the native-plantation forest boundary for the native wood species. However, a steep logistic relationship described the change in ordinal composition of *P. radiata* across the native-plantation forest boundary (Figure 3.6 E). Despite the change in ordinal composition the community composition of Coleoptera species colonising *P. radiata* did not change across native to plantation forest boundary (Figure 3.6 E). The community composition of beetles colonising *A. serrata* and *M. ramiflorus* did change linearly with proximity to interior native forest. Community composition in *S. digitata* dead wood changed logistically with proximity to native forest and showed a pronounced reduction in CAP axis 1 scores between 5m and 25m from the native-plantation forest boundary (Figure 3.6 F).

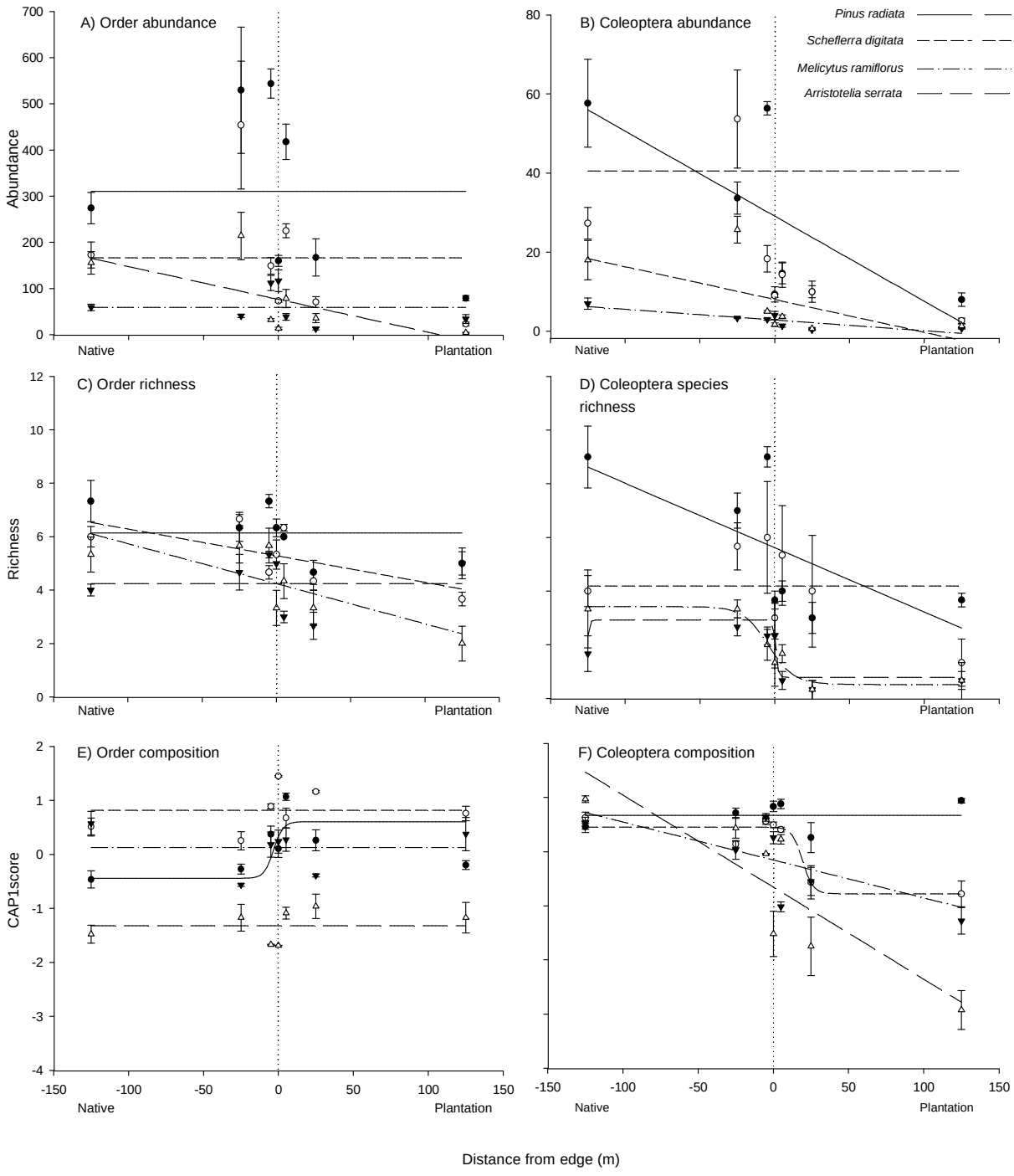


Figure 3.6 A) Taxonomic order and B) Coleoptera abundance, C) Taxonomic order and D) Coleoptera richness, and E) Taxonomic order and F) Coleoptera CAP axis1 score (±1 SE) along transect from inside native forest remnant (-125m) across edge (0m) and inside plantation forest (125m) habitat, for *P. radiata* wood (solid line and filled circles), *S. digitata* (short dashed line and hollow circles), *M. ramiflorus* (dashed and dotted line, filled triangles) and *A. serrata* (long dashed line and hollow triangles). All fitted lines indicate a significant change across the edge except null

lines (horizontal) which indicate no change in abundance, richness or community composition with distance from edge.

3.3.5 Wood species indicators

The indicator analysis provides resolution on which species and orders drive the differences in community structure between the different deadwood species. Six ordinal groups and eleven beetle species were strongly associated with specific dead wood species. The class Annelida and the orders Coleoptera, Diptera, Hymenoptera (wasps), Diplopoda and Acari were strongly associated with *P. radiata* wood as were the five Coleoptera species, *Xenocnema spinipes*, *Pachycotes peregrinus*, *Bitoma insularis*, *Crisius binotatus* and Coleoptera sp. 7 (Table 3.5). There were no invertebrate class or order associations for the three types of native wood. However, there were strong associations between *S. digitata* and the Coleoptera species *Xylotoles gratus*, *Mitrastethus baridioides*, Chryporichini sp. 49 and Coleoptera sp. 9. The Coleoptera species *Hypocryphalus* sp. 55 and *Phrynixus* sp. 41 were associated with *A. serrata* (Table 3.5). There were no significant indicator species for *M. ramiflorus* deadwood.

The organisms associated with *P. radiata* had the strongest indicator values ranging from 0.24 to 0.57 with four of the significantly associated orders and species having indicator values greater than 0.5 (Table 3.5). By comparison Coleoptera species that were associated with native wood species had lower indicator values, 0.20 and 0.24 for the two species associated with *M. ramiflorus* and 0.24 to 0.34 for the four Coleoptera species associated with *S. digitata* (Table 3.5).

Table 3.5 Order groups and Coleoptera species with their maximum indicator value (indval) in an indicator species analysis, the wood species (indcls) this applies too, the P-value (p-val) and the significance of this indicator value: "***" ≤ .001, "**" ≤ 0.01, "*" ≤ .05. Only those that are significant (P ≥ 0.05, IndVal ≥ 0.2) indicators of different wood types are displayed here, see Appendix 3.3 for full indicator results.

Taxonomic group	**IndVal**	**IndCls**	**P-val**	**Significance**
Diptera	0.57	*Pinus radiata*	0.001	***
Coleoptera	0.56	*Pinus radiata*	0.001	***
Hymenoptera (other/wasps)	0.52	*Pinus radiata*	0.001	***
Acari	0.32	*Pinus radiata*	0.045	*
Annelida	0.29	*Pinus radiata*	0.001	***
Diplopoda	0.29	*Pinus radiata*	0.002	**
Coleoptera species	**IndVal**	**IndCls**	**P-val**	**Significance**
Hypocryphalus sp. 55	0.24	*Aristotelia serrata*	0.005	**
Phrynixus sp. 41	0.20	*Aristotelia serrata*	0.021	*
Xenocnema spinipes	0.57	*Pinus radiata*	0.001	***
Pachycotes peregrinus	0.48	*Pinus radiata*	0.001	***
Bitoma insularis	0.41	*Pinus radiata*	0.001	***
Sp. 7	0.26	*Pinus radiata*	0.002	**
Crisius binotatus	0.24	*Pinus radiata*	0.002	**
Mitrastethus baridioides	0.34	*Schleffera digitata*	0.006	**
Cryptorhychini sp. 49	0.29	*Schleffera digitata*	0.001	***
Xylotoles gratus	0.29	*Schleffera digitata*	0.001	**
Sp. 9	0.24	*Schleffera digitata*	0.003	**

3.4 Discussion

Understanding the relative importance of stand and landscape scale factors as drivers of saproxylic invertebrate diversity is necessary to support biodiversity conservation in managed forests to. I found that both local and landscape scale factors play an important role in structuring saproxylic communities. There was a marked difference in the community composition of saproxylic invertebrates colonising experimental *P. radiata* billets compared to native dead wood billets, however this effect was not consistent across the stand boundary. Although there was no overall difference in the species richness (rarefaction) of different wood types, edge response functions showed linear and non-linear declines in the ordinal and Coleoptera species richness of both native and exotic wood species with increasing distance from interior native forest sites. Similar changes in community composition were also observed in the transition from native forest to plantation stands.

3.4.1 Community structure primarily driven by wood species

Wood species was the most important factor structuring Coleoptera within deadwood. This is consistent with others that found distinct differences in Coleoptera species composition between different tree species that weremost pronounced when comparing coniferous and broadleafed tree species (Lindhe and Lindelow 2004, Lindbladh et al. 2007, Jie et al. 2008). Most species that had a strong association with one particular wood species were associated with the exotic *P. radiata*, the only coniferous tree species in our study. However, *Xylotoles gratus*, *Mitrastethus baridioides*, Chryporichini sp. 49 and Coleoptera sp. 9 were associated with the native tree *S. digiatata* and *Hypocryphalus* sp. 55 and *Phrynixus* sp. 41 were associated with *A. serrata*.

The large number of species (particularly Coleoptera) that colonise *P. radiata* suggests there is a subset of the native saproxylic fauna that has switched from some native wood source to the novel *P. radiata*. It is possible that some New Zealand invertebrates have evolved cues to search for native soft wood species such as podocarps (another group of conifers) which were dominant in the study area prior to the clearance of native forest (Nicholls 1991). Probably the best example of a host shift to the exotic *P. radaiata* is the cerambycid *Prionoplus reticularis*. This species reaches extremely high abundances in *P. radiata* plantations. This species was not recorded in the young logs used in this study but was recorded in older *P. radiata* material (Chapter 2).

The minor differences in species richness between wood species is consistent with Jie et al. (2008)who found significant differences in the number of saproxylic beetle species found living in different log species. However, others have found no differences in saproxylic species richness between tree species, even when those trees have very different relative abundances in forest stands (Lindhe and Lindelöw 2004, Ulyshen and Hanula 2009b). As yet there is no known reason for the lack of congruence between such studies, however my study focussed on both native and exotic wood species. The lack of evolutionary history between the native saproxylic fauna and *P. radiata* could partially explain these differences.

The presence of a unique assemblage of saproxylic species that specialize on the wood of native understory tree species highlights the importance of this resource for maintaining biodiversity within managed landscapes. Individual preferences by particular invertebrates for different wood may be due to differences in wood properties such as soft wood conifers versus harder broadleaf native wood. In some cases bark characteristics may also play a role, for example, adults of *M. baridioides* seek shelter under bark and so do those of *Ptinella cavelli* (Johnson 1982) and both of these species are associated with *A. serrata*. The unique

bark characteristics of this species may provide a habitat prefereable to that of the other wood species. It is not as thick as that of *P. radiata* and comes loose more readily, but is more durable and was more often intact than that of *M. ramiflorus* and *S. digitata* when the billets were collected (Personal observation).

3.4.2 Proximity to native habitat drives community structure

There was a clear influence (although not as important as tree species) of proximity to native habitat on saproxylic invertebrate communities. Ordinal community composition in *P. radiata* wood showed a significant non linear response to native forest proximity with most change occuring at the habitat boundary. However, ordinal composition in native wood billets was not affected by proximity to native habitat. Although the effect of proximity was only a marginally significant predictor of Coleoptera community structure when assessing all wood types simultaneously, individual edge response functions showed clear declines in species richnes and changes in community composition and with distance from native forest habitat. This is consistent with earlier work on ground beetles that found native habitat proximity to have important effects on community composition within *P. radiata* plantations (Pawson et al. 2008). The change in community composition and the reduced taxonomic richness of invertebrate orders and Coleoptera species for some wood types as a function of increasing distance from interior native forest habitat suggests that both resource availability and landscape scale variables are important factors structuring saproxylic invertbrate communities in plantations.

Some have argued that altered beetle community structure in small remnants is primarily driven by changes in microclimate caused by habitat edges (Grimbacher et al. 2006). Edge effects relating to altered microclimate have been shown to be a major determinant of

vegetation dynamics in fragmented lowland forests in New Zealand (Young and Mitchell 1994). Indeed, edge effects can extend up to 300m and are key process altering biomass dynamics at forest edges causing elevated mortality of large trees leading to increased woody debris and litter (Laurance et al. 1998, Nascimento and Laurance 2004). The effects of both habitat type and dead wood species found in this study may partially or wholly reflect such microclimatic differences between native forest and regenerating *P. radiata* standsFuture work should concentrate on disentangling these effects by conducting paired studies of deadwood in native forest adjacent to both regenerating and mature *P. radiata* stands

3.4.3 Wood species effects on beetle richness are dependant on proximity to native habitat

Coleoptera species richness was consistently higher in native forest as opposed to regenerating plantation stands. This contrasts with Swedish research in managed forests that showed that sun exposed high stumps have a greater species richness than those with less sun exposure (Lindhe and Lindelow 2004). However, these stump species were not compared in the seperate habitats whereas I compared exotic plantation stands with native forest habitats. In my study the effect of tree species was mediated by habitat types (native or plantation). For example, *Pinus radiata* and two of the native wood species had higher beetle species richness when placed in native forest compared to adjacent plantation stands.. While I expected there to be some habitat dependence I hypothesised that native wood billets would have the greatest species richness in native habitats. It is unclear why beetle species richness in *P. radiata* wood was greater in native habitat. This may be due to a number of factors including log size as the pine billets were larger than the native wood. Literature suggests larger logs consistently host a greater species richness which may be due to the greater number of micro-habitats in wood of larger size (Lindhe and Lindelow 2004, Grove and

Forster 2011). Alternativelythe higher abundance/richness in native forests could be a reflection of resource scarcity whereby individuals that have dispersed from plantation stands into native forest are concentrated onto the experimental billets as there is no other *P. radiata* available in the native forest. Furthermore differences in microclimatic between native and regenerating plantation forest stands could be important. Studies in Europe have shown that microclimate, e.g., sun-exposure has a significant influence the breeding success and thus community composition and richness of saproxylic communities in deadwood(Lindhe and Lindelöw, 2004)

3.4.4 Conclusions and implications

This research has shown clear differences in the species composition associated with different dead wood species and their proximity to interior native forest habitat. Furthermore, elements of the native fauna have clearly switched from their natural host tree species and are able to maintain high population densities on *P. radiata* dead wood material. Species colonising deadwood fall into two broad categories, those that are associated with native habitat and those that are habitat generalists occupying both native and plantation habitats. The unique communities associated with the understory flora of plantation forests and those restricted to native remnants highlight the importance of these features for maintaining saproxylic diversity at the landscape scale.

Because of the increasing global energy demands and pressure to find alternatives to fossil fuels, forest managers are beginning to remove wood (such as stumps) that in the past would have been left after harvesting (Bengt 2006, Hjältén et al. 2010). This has been heavily adopted in Europe, particularly Scandenavia, and is now being evaluated for large scale adoption in New Zealand (Hall and Gifford 2008). This created a tradeoff between

biodiversity conservation and economics and it is vital that sufficient dead wood is retained in such a way that biodiversity benefits are retained (Jonsson et al. 2005). Therefore, dead wood of a variety of species and in close proximity to native forest remanants should be a priority for retention. Furthermore, if altered microclimatic effects are a primary driver of arthropod response to forest fragmentation, then retained thinning residues in closed canopy forests could be used to enhance biodiversity in areas surrounding remnant native habitat as some saproxylic species would colonise dead wood in the adjacent plantation stands. In addition, this is likely to assist rare species that are worst affected by habitat loss, due to poor dispersal abilities (Jonsson et al. 2005, Buse 2011), by providing a resource subsidy in close proximity to the native forest remnants.

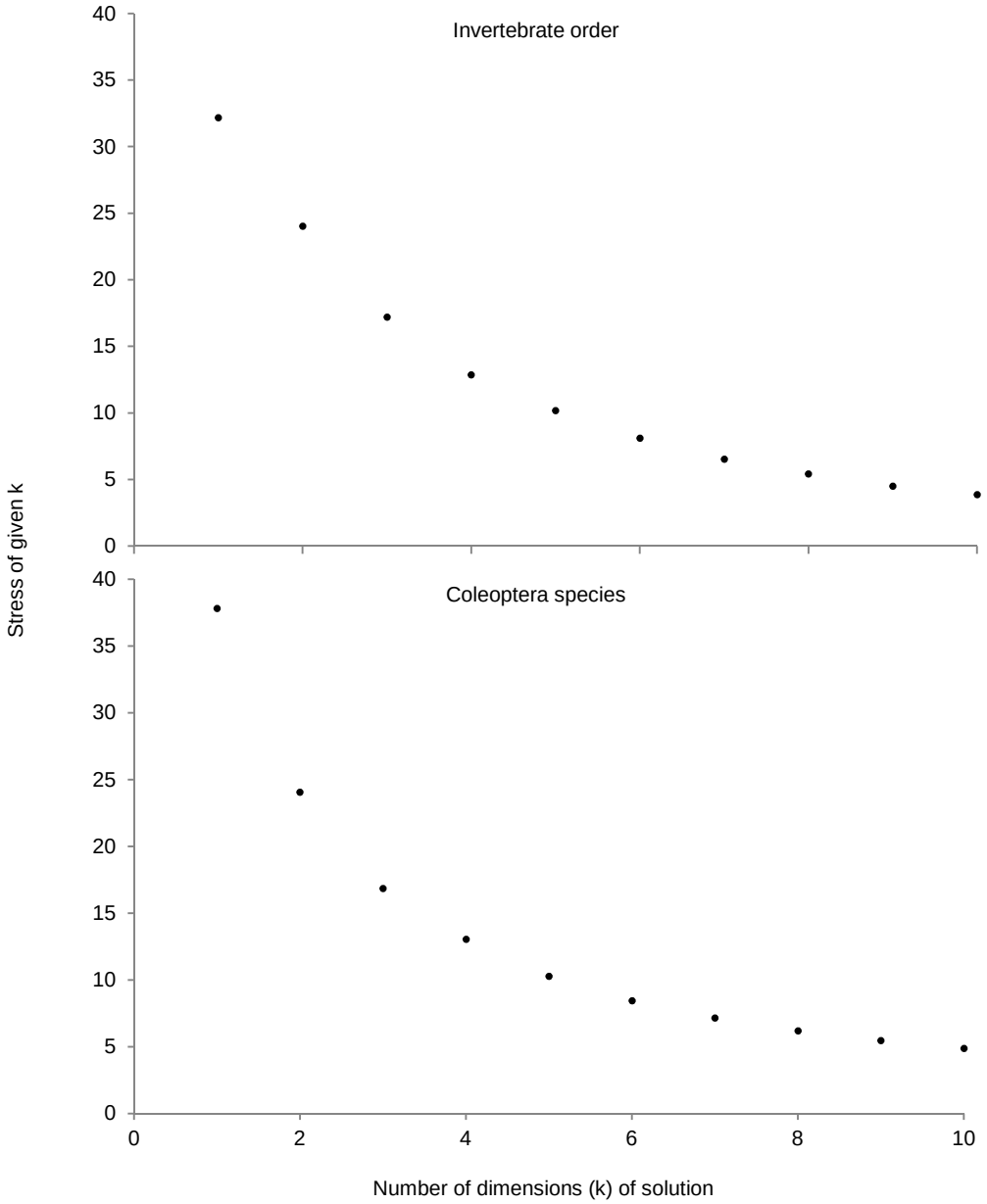
In terms of forest management, it has been recommended to thin stands to create a mosaic of dense thickets and relatively open areas, including heavy thinning of some areas early in the rotation to stimulate a diverse understory flora and associated fauna (Hartley 2002). Varying the timing and intensity of thinning creates increased diversity in the age of dead wood and stimulates understory plant development in heavily thinned areas. Enhancing plant diversity has the flow on effect of creating a greater diversity of wood species. This combination of different aged deadwood resources and varying species is an important strategy for maintaining high levels of saproxylic diversity throughout the landscape. Because of the importance of proximity to native habitat it would be most beneficial to apply such management strategies in stands adjacent to native forest remnants.

The clear decreases in abundance and richness of saproxylic invertebrates with increasing distance from interior native forest habitat highlights the importance of native remnants within plantations as habitat for native species. The New Zealand Forest Stewardship Council (FSC) certification scheme will require 10% native habitat as ‘set asides’ within plantations

when the standard is approved by the international FSC (Anon 2011). The proportion of plantation that must be set aside has been a contentious issue (Horner 2011). My results provide further evidence that these ‘set asides’ are important habitat for biodiversity within plantations. However, additional work will be required to understand the relationship between the proportion of ‘set asides’ in plantations and the benefits to biodiversity conservation. What is apparent from this study is that the proximity to native habitat is clearly more important for Coleoptera species that colonise native wood resources in the plantation understory as opposed to those that colonise *P. radiata*. Thus retaining native wood species in the understory of stands that are in close proximity to native fragments may provide an important resource subsidy for saproxylic populations in small remnant native forests patches.

3.5 Appendices

Appendix 3.1 Scree diagrams used to judge appropriate number of dimensions for NMDS. Solutions selected were: K = 4 Stress = 12.86 (Order data) and K = 4, Stress = 13.06 (Beetle data).



Appendix 3.2 A) Fitted continous and categorical variables to NMDS ordination of adult Coleoptera species data. Significant variables of interest were used in a CAP with significant variables that were not of interest partialled out using the condition command in the *capscale* function. B) Models with constraining and conditional variables used in *capscale.*

A) Fited environmental variables to NMDS ordinations

	Invertebrate order			Coleoptera species		
Variable	**r2**	**Pr(>r)**	**Significance**	**r2**	**Pr(>r)**	**Significance**
Proximity	0.02	0.448		0.137	0.005	**
Dead wood abundance	0.005	0.836		0.0816	0.052	.
Litter abundance	0.003	0.886		0.0807	0.067	.
Moisture	0.029	0.299		0.0516	0.165	
Aspect	0.058	0.094	.	0.0661	0.106	
Slope	0.001	0.957		0.0377	0.277	
Latitude	0.000	0.97		0.1003	0.027	*
Longitude	0.000	0.975		0.1028	0.024	*
5000 m buffer	0.001	0.961		0.0999	0.028	*
2000 m buffer	0.015	0.573		0.0678	0.099	.
1000 m buffer	0.009	0.709		0.0968	0.035	*
500 m buffer	0.016	0.515		0.0811	0.068	.
200 m buffer	0.004	0.845		0.0736	0.075	.
100 m buffer	0.006	0.79		0.0517	0.157	
Pine age	0.005	0.816		0.0829	0.06	.
Volume	0.003	0.888		0.0176	0.526	
Mean annual temperature	0.002	0.942		0.0962	0.03	*
Proximity * Wood species	0.083	0.031	*	0.0078	0.786	
Dead wood species	0.048	0.262		0.2645	0.001	***
Landscape	0.009	0.847		0.0657	0.053	.
Artificial shade	0.038	0.043	*	0.0623	0.01	**

B) models used for constrained ordination

capscale(formula=log(orders+1)~Wood*P+Condition(Shade),data=EnvironO,proximity="bray")

```
capscale(formula=log(Beetles2+1)~Wood+Proximity+Condition(Y,Shade),data=EnvironB,pr
oximity="bray")
```

Appendix 3.3 Full wood species indicator results for taxonomic groups and Coleoptera species.

Taxonomic group	IndVal	IndCls	P-val	Significance
Isopoda	0.19	*Aristotelia serrata*	0.012	*
Hymenoptera (Formicidae)	0.19	*Aristotelia serrata*	0.014	*
Annelida	0.29	*Pinus radiata*	0.001	***
Coleoptera	0.56	*Pinus radiata*	0.001	***
Diptera	0.57	*Pinus radiata*	0.001	***
Hymenoptera (other/wasps)	0.52	*Pinus radiata*	0.001	***
Diplopoda	0.29	*Pinus radiata*	0.002	**
Acari	0.32	*Pinus radiata*	0.045	*
Lepidoptera	0.22	*Pinus radiata*	0.197	
Dermaptera	0.07	*Pinus radiata*	0.435	
Aranae	0.05	*Pinus radiata*	0.789	
Hemiptera	0.06	*Pinus radiata*	0.919	
Pseudoscorpiones	0.17	*Schleffera digitata*	0.062	.
Chilopoda	0.14	*Schleffera digitata*	0.295	
Collembola	0.30	*Schleffera digitata*	0.448	
Coleoptera species	**IndVal**	**IndCls**	**P-val**	**Significance**
Hypocryphalus sp. 55	0.238095	*Aristotelia serrata*	0.005	**
Phrynixus sp. 41	0.197802	*Aristotelia serrata*	0.021	*
Cryptorhychini sp. 39	0.153846	*Aristotelia serrata*	0.088	.
Psepholax sp. 37	0.095238	*Aristotelia serrata*	0.216	
Sp. 33	0.047619	*Aristotelia serrata*	1	
Sp. 46	0.031746	*Aristotelia serrata*	1	
Sp. 54	0.047619	*Aristotelia serrata*	1	
Sp. 56	0.047619	*Aristotelia serrata*	1	
Sp. 77	0.142857	*Melicytus ramiflorus*	0.061	.
Staphlinidae sp. 2	0.098456	*Melicytus ramiflorus*	0.851	
Sp. 27	0.047619	*Melicytus ramiflorus*	1	
Sp. 28	0.047619	*Melicytus ramiflorus*	1	
Sp. 29	0.047619	*Melicytus ramiflorus*	1	
Sp. 43	0.047619	*Melicytus ramiflorus*	1	
Xenocnema spinipes	0.571429	*Pinus radiata*	0.001	***
Bitoma insularis	0.40553	*Pinus radiata*	0.001	***
Pachycotes peregrinus	0.47619	*Pinus radiata*	0.001	***
Sp. 7	0.263736	*Pinus radiata*	0.002	**

Crisius binotatus	0.238095	*Pinus radiata*	0.002	**
Sp. 15	0.190476	*Pinus radiata*	0.014	*
Pycnomerus sophorae	0.142857	*Pinus radiata*	0.067	.
Sp. 50	0.140625	*Pinus radiata*	0.087	.
Sp. 44	0.095238	*Pinus radiata*	0.222	
Sp. 17	0.095238	*Pinus radiata*	0.227	
Sp. 40	0.095238	*Pinus radiata*	0.262	
Staphlynidae sp. 8	0.14652	*Pinus radiata*	0.264	
Staphlinidae sp. 1	0.095238	*Pinus radiata*	0.265	
Cryptamorpha brevicornis	0.069264	*Pinus radiata*	0.608	
Sp. 2	0.047619	*Pinus radiata*	1	
Sp. 3	0.047619	*Pinus radiata*	1	
Zeoleusis virgula	0.047619	*Pinus radiata*	1	
Sp.10	0.047619	*Pinus radiata*	1	
Sp. 12	0.047619	*Pinus radiata*	1	
Sp. 14	0.047619	*Pinus radiata*	1	
Sp. 18	0.047619	*Pinus radiata*	1	
Sp. 26	0.047619	*Pinus radiata*	1	
Sp. 53	0.02381	*Pinus radiata*	1	
Sp. 68	0.015873	*Pinus radiata*	1	
Bitoma distans	0.047619	*Pinus radiata*	1	
Ablabus sp. 72	0.047619	*Pinus radiata*	1	
Cossoninae sp. 76	0.047619	*Pinus radiata*	1	
Hylastis ater	0.047619	*Pinus radiata*	1	
Cryptorhychini sp. 49	0.285714	*Schleffera digitata*	0.001	***
Xylotoles gratus	0.285714	*Schleffera digitata*	0.001	**
Sp. 9	0.238095	*Schleffera digitata*	0.003	**
Mitrastethus baridioides	0.344296	*Schleffera digitata*	0.006	**
Cossoninae sp. 47	0.108844	*Schleffera digitata*	0.053	.
Anthribidae sp. 63	0.142857	*Schleffera digitata*	0.067	.
Sp. 45	0.119048	*Schleffera digitata*	0.144	
Sp. 62	0.095238	*Schleffera digitata*	0.243	
Ptinella cavelli	0.209524	*Schleffera digitata*	0.281	
Sp. 67	0.089286	*Schleffera digitata*	0.39	
Sp.4	0.063492	*Schleffera digitata*	0.606	
Sp. 34	0.047619	*Schleffera digitata*	1	
Sp. 35	0.047619	*Schleffera digitata*	1	

Sp. 56	0.047619	*Schleffera digitata*	1
Sp. 60	0.02381	*Schleffera digitata*	1
Sp. 64	0.047619	*Schleffera digitata*	1
Sp. 66	0.047619	*Schleffera digitata*	1
Sp. 69	0.02381	*Schleffera digitata*	1
Micro-Staphylinidae	0.047619	*Schleffera digitata*	1

Chapter 4 General discussion

Forests currently cover 31% or 4 billion ha of Earth's landmass, however forest loss is a major causal agent of biodiversity loss that is expected to continue due to the ever growing human population (Sala et al. 2000, Fahrig 2001, Brook et al. 2003). Global forest area declined by 13million ha annually in the last decade, however during the same period the area of planted forests increased by approximately 5 million ha annually (FAO 2010). This expansion of plantation forests is primarily driven by global demands for wood, wood fibre and bio-energy (Bengt 2006, Jonsell 2007). Although these plantations do not support the same biodiversity as natural forests (Barlow et al. 2007, Didham 2011) they do provide significant opportunities for a range of species including native birds (Clout and Gaze 1984, Barbaro et al. 2005, Deconchat et al. 2009, Seaton et al. 2010), understorey plants (Allen et al. 1995, Díaz et al. 1998, Brockerhoff et al. 2003, Brunet et al. 2011), and invertebrates (Mesibov 2005, Berndt et al. 2008, Pawson et al. 2008). Due to the heavily fragmented nature of many landscapes, including those in New Zealand (Ewers et al. 2006), it is becoming increasingly apparent that to halt or slow declines in biodiversity values will require greater integration of biodiversity conservation into production land uses (Norton 2001, Watson et al. 2011). To support this, research is required to quantify how specific management practices impact native biodiversity so that conservation and production outcomes can be achieved in plantation forests (Lindenmayer et al. 2006, Müller et al. 2010).

Globally researchers have assessed the impact of forest management actions and conservation management actions on the abundance and community composition of saproxylic species as a function of different tree species (Lindhe and Lindelow 2004, Jie et al. 2008, Ulyshen and Hanula 2009b), landscape elements (McGeoch and Gaston 2000, Lindbladh et al. 2007, Buse

2011) and deadwood decay stages (Siitonen 2001, Hammond et al. 2004, Brunet and Isacsson 2009) on saproxylic invertebrates. However, most research has been conducted in natural forests (both managed and unmanaged) and further research that addresses the impact of specific management practices is required in intensively managed plantation forests at a scale that is relevant to forest managers (Lindenmayer et al. 2006).

Two broad categories of management actions have been suggested to improve biodiversity in plantation forests, 1) stand scale initiatives such as the selection of tree species, rotation length, stocking etc, and 2) landscape factors such as the spatial arrangement of stands and the proportion of, and proximity to, native habitat remnants (Hartley 2002, Lindenmayer and Hobbs 2004, Brockerhoff et al. 2008a).

My research assessed the influence of both stand and landscape scale factors on the species richness and composition of saproxylic invertebrates. At the stand scale the effect of dead wood age on saproxylic invertebrates was assessed across the complete spectrum of wood decay in a large-scale standardised space for time substitution experiment (Chapter 2). The importance of understory native woody vegetation as habitat for saproxylic invertebrates was assessed both at the stand and landscape scale by quantifying the importance of proximity to native habitat (Chapter 3).

4.1 The importance of dead wood age in structuring saproxylic invertebrates at the stand scale.

There is a complex interaction between saproxylic arthropods and fungi that results in a succession of species that are associated with biological (Müller et al. 2002, Persiani et al. 2010) and physical (Saint-Germain et al. 2007) changes in deadwood material as it decays. It

is well known that saproxylic invertebrates respond to the biophysical decay stage of snags (Brunet and Isacsson 2009) and fallen wood material (Vanderwel et al. 2006, Thomas et al. 2009) but it is unclear if these changes are reflected in the specific age of deadwood as this is difficult to measure without conducting long term experiments. However, in plantation forests accurate data exists that specifies the age of deadwood created by management actions such as thinning. Thus, in plantations deadwood age provides an objective measure by which forest managers can quantify saproxylic habitat availability throughout the landscape.

Forest thinning residues, which are currently retained in many plantation stands, were found to provide habitat for a range of native saproxylic invertebrate taxonomic groups. Species richness of higher taxonomic groups and Coleoptera species increased with deadwood age highlighting the importance of late decay stage wood in forest stands. These findings are consistent with overseas research that found greater diversity of saproxylic species in advanced decay stages (Heilmann-Clausen 2001, Vanderwel et al. 2006, Brunet and Isacsson 2009, Thomas et al. 2009) and has been attributed to increased microhabitat variation in older wood (Langor et al. 2008). However, they contrast with the work of Ulyshen and Hanula (2010) who found richer saproxylic communities in early decay stage wood. This may be due to a greater prevalence of host specific primary wood feeding invertebrates in early decay stage wood (Jie et al. 2008, Ulyshen and Hanula 2010). In New Zealand *Pinus radiata* is an exotic species and the low species richness in early decay stage wood is likely to reflect the lack of evolutionary history between *Pinus* spp. and the native saproxylic fauna.

The community structure of saproxylic invertebrates in *P. radiata* changed as a function of deadwood age. This matches the documented changes associated with different decay stages of deadwood (Vanderwel et al. 2006, Brunet and Isacsson 2009). Change in the community composition of saproxylic invertebrates followed a successional pathway from primary

deadwood feeders to a community dominated by fungal feeders, predators and parasitoids. This successional pathway has already been documented in other studies of saproxylic invertebrates (Gibb et al. 2006, Vanderwel et al. 2006, Johansson et al. 2007, Hjältén et al. 2010) but not clearly related to age of dead wood.

The unique fauna associated with different decay stages of deadwood suggests that biodiversity over a large scale will be maximised by having different aged stands in the landscape and subsequent deadwood ages. Additionally, it is important to understand how the spatial availability of deadwood over the landscape and size of cutovers affects this complex successional pathway. It is particularly important to understand how species with poor dispersal abilities, which are the most threatened by anthropogenic disturbance (Jonsson et al. 2005, Buse 2011), are impacted by this spatial arrangement.

4.2 The importance of understory native woody vegetation and proximity to native habitat for structuring saproxylic communities in different wood types.

Greater floristic diversity in a given area is often correlated with a greater diversity of fauna (Lindenmayer and Hobbs 2004). New Zealand plantations often have a rich understory flora (Allen et al. 1995, Ogden et al. 1997, Brockerhoff et al. 2003), however the importance of this flora for supporting other trophic levels, such as herbivores and saproxylic invertebrates, has not been quantified. Research has shown that many saproxylic arthropods are host specific where individual tree species often support different subsets of the total saproxylic community (Lindhe and Lindelow 2004, Lindbladh et al. 2007, Jie et al. 2008). Thus the presence of woody native understory plants may enhance the diversity of saproxylic beetles in plantation stands.

I found that the community structure of saproxylic fauna colonising deadwood was dependent on tree species identity. Furthermore, deadwood from the exotic conifer species *P. radiata* supported a different assemblage of saproxylic species compared to the native woods studied. This is consistent with research on stumps in Europe (Lindhe and Lindelow 2004, Lindbladh et al. 2007) and stem and branch material in China (Jie et al. 2008) that show pronounced differences in the community structure of saproxylic invertebrates associated with conifers and broadleaved tree species. The distinct assemblage supported by understory native tree species highlights the contribution that production land uses make to conserving biodiversity in fragmented landscapes. However, the importance of this understory resource may be limited by landscape factors as the Coleoptera species richness of 2 of the 3 native species declined with distance from native forest. In addition the community structure of Coleoptera colonising all three native tree species changed significantly from native forest to regenerating plantation stands. The decline in species richness colonising native deadwood was not linear and showed a step change at the native forest – plantation boundary. This would indicate that there is a fundamental difference in the suitability of regenerating plantation stands for some saproxylic species. The species present in these plantation systems are likely to possess good dispersal abilities as they must be tolerant of periodic disturbance from harvesting (Pawson et al. 2009, Pawson et al. In Press). Thus the differences I observed in species richness as a function of proximity to native habitat may reflect the contrast between open and closed forest. Similarly the lack of any effect of the proportion of native habitat on the community structure of different aged dead *P. radiata* probably reflects the strong dispersal ability of species which colonise all closed pine forest in the study area. This is consistent with research findings from European forests that found stand factors (open vs closed) were more important predictors of saproxylic communities than landscape factors (McGeoch et al. 2007).

The unique fauna associated with native wood and pine wood suggest that both of these deadwood resources will contribute to the overall diversity in a given area if retained. The proximity effect on richness suggests that this would be most beneficial in close proximity to interior native habitat. While the unique community structure seen in the recent cutovers studied suggest deadwood resources provide benefits in clearfells, they may provide more important resource subsidies when retained in closed plantations in close proximity to interior native forest because of the clear microclimatic effects observed. This may even provide supplementary habitat to species with poor dispersal abilities and warrants further study.

4.3 Implications for sustainable forest management

The dominant conservation paradigm in managed forests is to retain large volumes of dead wood to maintain biodiversity (Jonsson et al. 2005, Lassauce et al. 2011). However, increasing global energy demands and pressure to find alternatives to fossil fuels are promoting increased removal of woody debris from forests after harvesting and thinning . In the past such wood would have been left where it would provide habitat for saproxylic species (Bengt 2006, Hjältén et al. 2010). The prospect of increasing residue removal creates a tradeoff between biodiversity conservation and production, and it is vital that sufficient dead wood is retained to ensure the biodiversity values of stands are not compromised(Jonsson et al. 2005). However, setting such limits on woody residue extraction is hindered by a lack of basic biological and ecological knowledge about most species (Jonsson et al. 2005, Langor and Spence 2006) and relevant research showing how management practices impact biodiversity at scales applicable to forest managers (Lindenmayer et al. 2006). In the near future it will be important to understand the relationship between deadwood volume in plantation stands and the population dynamics of saproxylic invertebrates.

Due to the strong relationship between saproxylic community composition and deadwood age it is important that forest managers maintain the greatest possible variation in deadwood resources. Large quantities of deadwood are only created at particular times in the stand rotation, for example harvesting, pruning and thinning, thus stand age can be used as a proxy of deadwood age in intensively managed plantations. Thus for the purposes of sustainable forest management reporting, such as Montreal Protocol and the Forest Stewardship Council, the inclusion of a statistic that quantifies the variation in stand ages across the entire plantation estate would be a suitable indicator of saproxylic invertebrate health in plantations. To take this concept further would require additional information on the volume of deadwood present as a function of stand age. Once available such data could be used to create a 'deadwood habitat availability' spatial layer to monitor changes in deadwood resources over time.

The differences in community composition and decline in Coleoptera species richness as a function of increasing distance from native forest habitat suggests that native remnants are a disproportionately important habitat for the conservation of saproxylic species in plantation landscapes. However, this may reflect the strong underlying microclimatic differences between my sampling points in native forest and young regenerating stands. Before firm conclusions can be made regarding the importance of native remnants relative to plantation as a whole, further research is required to assess the relationship between native habitat proximity and saproxylic community composition in older stands with equivalent microclimatic conditions.

4.4 Conclusions

Plantation forests offer significant opportunities for the conservation of biodiversity in fragmented landscapes. Diverse assemblages of saproxylic invertebrates are found in plantations relative to other production land uses, such as agriculture. Saproxylic invertebrates are functionally important in plantations as they play a key role in the decomposition of deadwood. Forest managers require empirical research that relates biodiversity values to specific management interventions. My findings show that local scale attributes are important for structuring saproxylic invertebrates, however such attributes must be expressed as quantifiable measures, at relevant scales, before they will be adopted by plantation forest managers. In this research I show that dead wood age is one such measure which could be used on a spatial basis to improve saproxylic biodiversity values in plantations. Furthermore, I show there is an interaction between local scale and landscape scale processes which structure biodiversity. Further, research is need to better understand how these processes contribute to biodiversity values through a better understanding on the dispersal limitations of saproxylic invertebrate in plantation forests.

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